SENSITIVITY OF WESTERN REDCEDAR TO CLIMATE AND WESTERN HEMLOCK LOOPER IN BRITISH COLUMBIA'S INLAND TEMPERATE RAINFOREST

by

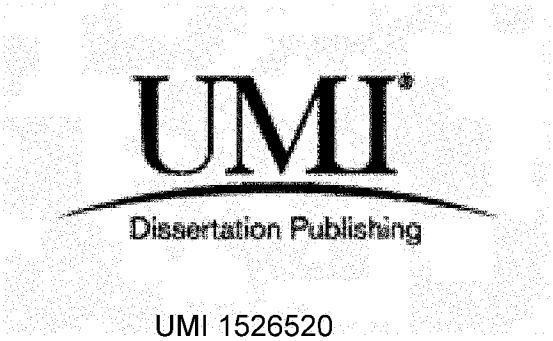
Christopher S. Konchalski

B.A. University of Northern British Columbia, 2009

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

December 2014



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Abstract

The inland temperate rainforest of British Columbia is a unique forest type dominated by large western redcedar. Uncertainty surrounding resilience of this forest to climate change and outbreaks of western hemlock looper makes development of management and conservation strategies challenging.

Western redcedar trees were sampled at paired low and higher elevation sites, on north and south-facing aspects. Western redcedar growth was positively correlated with January temperature and growing season precipitation, and was negatively correlated with June temperature. Reconstruction of western hemlock looper outbreaks demonstrated that successive years of warm, dry spring seasonal conditions preceded outbreaks, and the mean return interval was 36.5 years.

Western redcedar growth responded negatively to the same climate factors that were associated with looper outbreaks. Under a warmer and drier climate scenario, looper outbreaks are expected to increase in frequency, and western redcedar may not be able to survive defoliation as well as it has historically.

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Acknowledgements

This thesis is dedicated to my field assistants (both human and canine), all of my family across Canada, all of the UNBC dendro lab people (you know who you are), and my partner in life Vicky Serafini, who was diligent in reminding me that no matter what I was doing, I in fact should have been working on my thesis. Without you this wouldn't have been possible. And in a larger sense than this document, my sincere thanks go to my supervisor Dr. Kathy Lewis, who introduced me to the world of ecology and allowed me to discover places I would not otherwise have ever seen. Thank you.

CHAPTER 1. INTRODUCTION

1.1 The Inland Temperate Rainforest of British Columbia

The Inland Temperate Rainforest (ITR) of British Columbia (BC) is a highly productive forest type found in the interior of BC (Stevenson et al. 2011). It occurs along the lower slopes west of the Rockies at moderate elevations from the McGregor River watershed to the American border, beyond which its historical range persists only to a limited degree. The ITR provides an important timber supply for a number of forest districts, featuring the most productive site indices[1] in the interior of BC (Stevenson et al. 2011). Annual timber production throughout the forest is less than coastal forests, but higher than other interior forests (Stevenson et al. 2011). The dominant canopy species are western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg). The ITR bears likeness to coastal forests in its moisture regime and species composition (Ketcheson et al. 1991, Jull et al. 2001, Benson & Coxson 2002), despite having a continental climate. Although similar to their coastal counterparts in some respects, the wettest forests of the interior are unlike coastal forests in their disturbance regimes and regeneration dynamics (Arsenault & Goward 2000). The combination of continental climate, characterized by cold winters and a sustained snow-pack, and coastal levels of humidity provide the necessary moisture to sustain the species present (Arsenault and Goward 2000) and produce a fire return interval of up to 1000 years on some sites (Sanborn et al. 2006). The areas with the longest fire return intervals result in extremely old stands of trees and complex forest structure, and their disturbance regimes can become dominated by outbreaks of the

[1] Site index is a measure of the height at breast-height age 50 of the largest tree in a 0.01 ha plot (Mah & Nigh 2003).

defoliating insect western hemlock looper (*Lambdina fiscellaria lugrubrosa* Hulst) (Lepidoptera: Geometridae) (Hoggett 1998, 2002).

Western hemlock looper occurs in BC in most hemlock dominated and co-dominated stands and is considered to be one of the most destructive forest insects in the province. Western hemlock looper will defoliate all common tree, shrub, and herb species in the ITR during an outbreak (Hoggett & Negrave 2002). Although sometimes exhibiting temporal population cycles seemingly not connected to climate variables, defoliators in the insect order Lepidoptera are known to be sensitive to climate, and in many cases they exhibit cyclical population patterns driven by climate (Myers 1988). Climate-western hemlock looper relationships have not been explored in the ITR.

Trees are sensitive to pathogens and insects in various ways depending on the mechanism of damage. Defoliators such as western hemlock looper feed on the foliage of trees, reducing the tree's photosynthetic capacity. Trees then must use energy reserves to replace lost foliage; in successive years of defoliation, or singular years of extreme defoliation, reserves can be exhausted and lead to tree mortality (Loehle 1988). Trees respond to defoliation in several ways, including the production of deterrent compounds that may make foliage undesirable for consumption due to toxicity (Loehle 1988). One prominent detectable effect on trees by defoliators is the suppression of radial growth during and after outbreaks and this has been used to quantify insect outbreaks in temperate forests (Alfaro & MacDonald 1988; T. W. Swetnam & Lynch 1993; Bouchard et al. 2006)

1.2 History of the Inland Temperate Rainforest

The northern range of the ITR is part of the Caribou range of the Columbia mountains

and is geologically characterized by sedimentary and metamorphic rocks, particularly quartzite (Stevenson et al. 2011). The Fraser River drains the northern range of the ITR, with major tributaries being the Goat, McGregor, Torpy, and Bowron rivers. It is thought that the ITR became ice free sometime around 10,000 years before present (Lowden and Blake 1980). Soils of the Podzolic Order dominate the landscape of the ITR, with most of the parent material being the result of glacial movement. Ample moisture from the large winter snowpack throughout the growing season aids in litter decomposition producing characteristics similar to coastal soil properties (Stevenson et al. 2011).

The presence of typically coastal species such as western redcedar and western hemlock in the ITR is not fully explained in the scientific literature, as the vast area that separates the coastal and inland rainforests is climatically inhospitable for these species (Gavin et al. 2009). Several theories persist concerning the spread of inland rainforest species to their current range. The most robust theory suggests that cedar and hemlock spread into the ITR from glacial refugia in what is now Montana. Limited lake sedimentology in the ITR has explored the presence of pollen in lake cores (Gavin et al. 2009). Post glaciation, *Betula* spp., *Pinus* spp., and *Picea* spp. migrated to the ITR first (Gavin et al. 2009), with western hemlock and western redcedar following slowly afterwards. Western redcedar appeared in sediment cores only about 2000 years before present, suggesting that relatively recent and subtle climatic shifts may have allowed cedar to survive in the ecosystem. In addition, the pollen of western redcedar disperses over short distances compared to other species such as pines (Gavin et al. 2009), contributing to the slow post glacial recolonization of the ITR by western redcedar.

The ITR was used by various First Nations groups for centuries before colonial times.

The region was primarily a place to gather food such as salmon and berries, as well as for hunting. Permanent settlements were uncommon along the banks of the Fraser River although pit houses can still be found in the forest (Stevenson et al. 2011). Several local economies depend on the ITR for forest products, as the main employment of the region is in the forest industry. The ITR is a part of the Prince George Forest District's allowable annual cut (AAC) (BCMOF 2010). The neighboring forest district of McBride also depends heavily on the ITR for forest products (BCMOF 2010).

1.3 Uncertainty about Future Forest Response

A large amount of uncertainty surrounds the future of the ITR. Climate models vary in predictions about change in biogeoclimatic envelopes, and by extension floral composition, and are dependent on the assumptions made about which climate variables are most important and how trees and other plants will respond to predicted climatic changes. Predictions using ClimateBC software (Wang et al. 2006) show a substantial increase in the range of ecosystems featuring western redcedar, a dominant canopy species in the ITR, beyond its current range in BC (Hamann and Wang 2005). Other research has speculated that the range of the Interior Cedar-Hemlock biogeoclimatic zone will shrink due to drier conditions, being replaced by interior Douglas-fir forests (Hebda 1995). There is general agreement that trees in the Interior Cedar-Hemlock zone are sensitive to climate variables (Hebda 1995, 1997), but there is little agreement about future forest responses to changing climate. Forest sensitivity to climate variables and changes in disturbance regimes must be understood in order to predict future forest response to climate change in the ITR.

1.4 Purpose and Objectives

In order to help predict future forest ecosystem responses to climate change, it is necessary to assess the sensitivity and response of a dominant canopy species to variables such as climate and insect outbreaks. Western redcedar is one of the two dominant conifer species in the ITR and will be used to study the relationships between climate and tree growth, climate and western hemlock looper outbreaks, and interactions among western hemlock looper outbreaks, western redcedar growth, and climate within the northern ITR.

The objectives of this study are to:

1. Quantify the effects of climate variables and western hemlock looper on the radial growth of western redcedar in British Columbia's Inland Temperate Rainforest in a variety of topographic settings.
2. Explore the potential correlation between climate variables and western hemlock looper outbreaks in western redcedar.
3. Inform predictions of future climate impacts on western redcedar in the Inland Temperate Rainforest.

1.5 Layout of Thesis

This initial chapter is intended to give a broad overview of the entire study topic. Chapter 2 is a literature review that provides an overview of the body of scientific knowledge of the study topic, and outlines where more information is needed. Chapter 3 identifies the climate variables that have a significant effect on western redcedar growth and identifies trends in how trees are sensitive to those variables at various landscape positions. Chapter 4

provides a reconstruction of past outbreaks of hemlock looper and analyzes the climate variables that precede western hemlock looper outbreaks. Finally, chapter 5 examines interactions between western redcedar, climate, and western hemlock looper outbreaks in the ITR.

CHAPTER 2. LITERATURE REVIEW

2.1 Western Redcedar

Western redcedar is a widely distributed, scaly-leaved evergreen tree (Klinka & Brisco 2009). Its maximum height is approximately 60 m and it is BC's provincial tree. Western redcedar-dominated stands are often driven by gap dynamics, and its shade tolerance allows for a slow canopy recruitment rate in a patchy form on the landscape (Klinka & Brisco 2009; Kayahara et al. 1997). Western redcedar is prized for its unique wood properties, color, and odour. Western redcedar are long lived and can be older than 1000 years, leaving evidence of historic use by First Nations from bark stripping activities (Klinka & Brisco 2009). Literature on the silvics of interior western redcedar is limited (Robison 2000), and new information on the climate-growth relationship for interior western redcedar would shed light on potential future climate change implications for its geographic range.

2.1.1 Ecology of Western Redcedar

Western redcedar response to climate is well described in coastal BC (Klinka & Brisco 2009; Kayahara et al. 1997). Western redcedar has a wide edaphic amplitude, but is most productive on fresh to moist nutrient-rich soils (Klinka & Brisco 2009). In the drier portions of the interior, western redcedar persists in fire–dominated seral ecosystems as well as very wet, cold ecosystems in the northern interior of its range (Jull et al. 1998; Arsenault & Goward 2000 Stevenson et al. 2011). The most productive western redcedar stands occur in areas with ample moisture available. On the coast, the majority of the moisture comes in the form of precipitation as rain. Conversely, in the ITR, snowpack is thought to take on a

much greater role in feeding the hydrological cycles that sustain the species present in those ecosystems (Arsenault & Goward 2000).

2.2 Disturbance Regime of the Inland Temperate Rainforest

Disturbance is an important element in forest systems and influences canopy species present, as well as stand age and herb and shrub layer composition (Delong 2007). Disturbances can be caused by biotic and abiotic agents, such as insect outbreaks and fire, and can be at the scale of landscape to small forest gaps. Disturbance influences the regeneration dynamics of a stand of trees by causing mortality or suppression in trees, subsequently regulating the available light, water, and nutrients (Alfaro et al. 1999). Regeneration dynamics of western redcedar are poorly understood. Traditionally it was thought that western redcedar needed large scale disturbance to regenerate; however, more recent research has shown that shade is beneficial and that low seedling counts can be normal given that individuals can survive in the understory for centuries (Daniels 2003).

The most important abiotic disturbance agent in the ITR is fire (Arsenault & Goward 2000). Weather events such as wind and lightning also cause disturbances in the ITR. Fire return interval is defined as the period of time between two fire events in a specific area. The fire return interval can be further broken down into the composite fire return interval (period of time between fires that scarred or killed trees based on pre-determined parameters such as percentage of trees affected) and point fire return interval (period of time between two successive fires at a specific spatial point) (Speer 2010). Fire is thought to be uncommon in the wettest portions of the ITR, with a median point fire return interval estimated at 800-1200 years (Sanborn et al. 2006), however small, less intense fires are thought to be more

common. Fire is most common in the drier portions of the ITR found in the south; research has shown that the historical fire return interval around Glacier National Park in the ITR was about 80 years, however this has shifted to about 110 years, potentially due to the influence climate (Johnson et al. 1990).

The most important biotic disturbance agent in the ITR is western hemlock looper (WHL) (Alfaro et al. 1999; Hoggett 2000; Hoggett & Negrave 2002), which caused a cumulative defoliation of 39,000 ha during the 1990s and 45,000 ha during the 1950s in the northern range of the ITR.

2.2.1 Western Hemlock Looper and the Inland Temperate Rainforest

WHL occurs in most hemlock dominated and co-dominated stands in BC and is considered to be one of the most destructive forest insects in the province. Caterpillars feed on foliage of virtually any species (both coniferous and broadleaved trees) as it ascends into the canopy over the summer (Furniss & Carolin 1977), and will defoliate all known species during an outbreak (Hoggett & Negrave 2002). It has the potential to kill juvenile western redcedar, but it is atypical for a mature cedar to be killed in an outbreak, although it can happen (Alfaro et al. 1999). Although limited amounts of research have been done on the WHL, it is known to have killed large tracts of forest in the ITR historically (Hoggett 1999).

2.2.2 Ecology of Western Hemlock Looper

WHL adults lay their small (~ 1mm) oval eggs in mid-fall on a variety of substrates including bark and the duff layer on the forest floor (Alfaro et al. 1999) and lichen (Evenden et al. 1995). Eggs overwinter and hatch in spring or early summer and larvae begin feeding

on herbs, shrubs, and lower foliage before moving up the tree (Kinghorn 1954). Over the season they move to other sections of the tree and can damage large amounts of new and old foliage. The larvae are commonly called loopers or inchworms due to the looping motion employed by the insect to move (Hoggett 2000). WHL has six instars, or developmental stages, before pupation into the adult moth stage (Thomson 1957). Feeding is restricted to newly flushed buds for the first two instars, and from the third instar on, all ages of foliage is attacked. WHL are wasteful feeders, resulting in large amounts of forest damage despite relatively low populations (Hoggett & Negrave 2002). WHL outbreaks typically last for 2-4 years and are brought under control by an epizootic of a pathogenic nuclear polyhedrosis virus (Myers 1988) and wet conditions during flight (H. P. Koot 1994). Host availability is usually not the cause of decline of WHL populations. Aerial spraying has been employed in the United States as a means of controlling the insect, but this has not typically been employed in Canada (Furniss & Carolin 1977).

2.2.3 Climate and Western Hemlock Looper

In coastal British Columbia, warm, dry springs and early summers are conducive to the development of epidemic populations of WHL (McCloskey et al. 2009). Recent research using superposed epoch analysis of WHL outbreaks and climate near Vancouver, BC (McCloskey et al. 2009) showed that elevated temperatures in June preceded numerous outbreaks in the Lower Mainland. Given the shorter growing season found in the ITR, it is reasonable to hypothesize that July would be the important month for larval development in that ecosystem. Climate-western hemlock looper relationships have not yet been explored in the inland temperate rainforest to date.

2.3 Sensitivity of the Inland Temperate Rainforest to Climate Change

A great amount of uncertainty exists about the nature of climate change and its impacts on all ecosystems in British Columbia (Hebda 1997; Spittlehouse 2008). The potential effects of climate change on the ITR are poorly understood, and conflicting theories exist about its future (Hebda 1997). Some researchers believe that it will be adversely affected by a reduction in snowpack under a scenario of wetter but warmer winters (Hebda 1997), while others predict that the range of canopy species such as western redcedar will expand due to warmer temperatures (David L Spittlehouse 2008).

The range of western redcedar could greatly expand in response to warmer annual temperatures, supporting northward movement into what is traditionally the sub boreal spruce (SBS) and the boreal white and black spruce (BWBS) BEC zones (Hebda 1997); though its realized range may be smaller than its potential climatic envelope. These predictions are based primarily on examining temperature tolerance in western redcedar, and it is suspected that climatic changes such as increasing temperatures historically allowed western redcedar to colonize the ITR (Gavin et al. 2009). The ability of western redcedar to persist given drier winters and summers with less snowmelt is uncertain, and western redcedar-specific climate sensitivity parameters (e.g. temperature and precipitation – growth relationships) have not been characterized in the ITR.

2.3.1 Climate Data in Western Canada

Climate data in western Canada have been collected through various federally and provincially operated climate stations. Point-specific climate data are a valuable source of

information, but have some limitations, chiefly that stations are sporadically placed throughout the north-west of Canada, and can be at a distant location relative to study areas. In response to this, researchers (Daly et al. 2002) have created a product called PRISM, which interpolates data from climate stations throughout the US, adjusting for variables such as elevation and aspect. This product has been adapted for use in Canada and is called ClimateBC (T. Wang et al. 2006). Although in theory a regional climate signal can be better obtained using interpolated data, the problem persists that a small number of climate stations, often with incomplete records, are driving the interpolated values. The most complete climate record relatively close to the study area in the ITR is the Prince George A climate station (Station ID 1096450, 53.9° lat, -122.7° lon) (Environment Canada 2012), which covers the timespan of 1918 to present, and has been adjusted to have no missing values.

2.4 Dendrochronology

Dendrochronology is the study of tree rings across time (Stokes & Smiley 1968; Speer 2010). Principles underlying the science of dendrochronology include uniformitarianism, which states that the processes that occurred in the past are the same as the processes occurring today, such as trees responding favorably or unfavorably to climate variables like temperature or precipitation (Speer 2010). The principle of limiting factors states that tree growth will primarily reflect the variable or variables most strongly limiting their growth, e.g., temperature or precipitation (Speer 2010). The principle of cross-dating states that if tree rings from different trees of the same species are compared, then the accuracy of the assignment of calendar years can be verified and any errors in annual ring determination can be eliminated (Speer 2010). Using tree ring techniques with statistical

analyses, individual tree ring series, stand-level chronologies and climate data can be used to assess and quantify western redcedar's response to climate variables and reconstruct past WHL outbreaks. Western redcedar has been shown to display radial suppression during WHL outbreaks, leaving evidence of the event in the tree ring series (McCloskey et al. 2009). For that reason, western redcedar serves as a good recorder of historic WHL outbreaks that precede records of observed forest insect outbreaks.

Dendrochronology can be used to quantify the growth response of western redcedar to past western hemlock looper disturbance in both live and dead trees, and provide the basis for analysis of disturbance regimes and characteristics at the landscape level in the ITR (Fritts & Swetnam 1989). In the case of old trees having survived multiple outbreaks of WHL, dendrochronology can also be used to quantify the periodicity and severity of outbreaks by extending the analysis beyond recorded outbreak periods, within the time span that the tree ring samples represent (H. C. Fritts & T. W. Swetnam 1989).

2.4.1 Dendroclimatology

Dendroclimatology is a large sub-branch of dendrochronology that encompasses all analyses of tree-climate relationships, as well as reconstructing past climate variables. Tree-ring characteristics, such as ring width, reflect the variability of environmental factors that limit tree growth (Fritts 1976; Fritts et al. 1991). When compared to observed climate data, tree rings can provide insight into the climate variables that limit growth and have the most predictive power for a study species (Speer 2010). Correlation analysis is an accepted method of screening multiple climate variables to assess which are most important for a study species in a particular location (Fritts 1976). Response function analyses are commonly carried out

for the same variable combinations used for development of correlation matrices in order to only report the combinations found to be significant (α=0.05). Response function analysis is a regression technique commonly used when examining climate variables and their effects on a given study species (Fritts & Xiangding 1986).

2.4.2 Dendroentomology

Dendroentomological studies of defoliators normally use a host versus a non-host approach to determine which periods of suppression in the host species are attributed to insects that cause reduction in growth due to defoliation. The effect of climate on the ring-width indices is reduced by subtracting a non-host species chronology, from individual host ring-width series (Swetnam & Lynch 1993). One assumption of this method is that both species respond to climate similarly, and this is tested using correlation or response function analysis, or assessed graphically. Because WHL is understood to be a generalist feeder, meaning that it feeds on a wide range of species including shrubs such as devil's club (*Oplopanax horridus*) in addition to primary hosts such as cedars and hemlocks (Thomson 1957), it can be difficult to locate a non-host near defoliated sites. However, there are sections of forest that are typically out of the range of WHL outbreaks (e.g., forests at higher elevations). Trees growing in the Engelmann spruce-subalpine fir (ESSF) BEC zone, immediately upslope of the ICH, may make a suitable non-host to be used in conjunction with western redcedar chronologies, as only a small percentage of the areas defoliated during recorded WHL outbreaks was in ESSF (Jull et al. 1998).

2.5 The Forest Health Triangle

The forest health triangle was adapted from the disease triangle (Stevens 1960); a concept in plant pathology that describes three absolutely necessary elements for a plant pathogen outbreak to occur: a susceptible host, a virulent pathogen, and a hospitable environment in which the pathogen can develop. The forest health concept acknowledges the three way interaction between the host, insect, and environment (Stevens 1960). This conceptual model can be applied to WHL outbreaks in the ITR, and then viewed through a lens of forest management (Delong 2007). Of particular interest to forest managers in the interior of BC is the interaction between the WHL and climate, a variable component of the environment, and the impact that the insect has on the host tree. Also of interest is the host's direct interaction with the environment, or climate, which may help explain temporal shifts in susceptibility to insects (Spittlehouse 2006b; Kliejunas et al. 2009) because certain climatic conditions can make trees more susceptible to pathogens and insects. The three-way interactions between western redcedar, western hemlock looper, and climate have not been explored in the ITR.

2.6 Research Significance

The future impacts of climate change on species range and ecosystem functions are difficult to predict (Spittlehouse 2006a; Kliejunas et al. 2009). Climate models are highly variable in their predictions of future climate scenarios, making it even more difficult to predict how plant communities will respond to these changes (Hamann & T. L. Wang 2005). Furthermore, plant sensitivity trade-offs between climatic variables are poorly understood in regions such as the ITR. For example, the relative benefit to tree growth of an increase in

temperature versus the relative reduction in growth due to limited moisture is poorly understood (Stevenson et al. 2011) and will vary among species and location. By assessing species-specific climatic responses, the confidence in predicting how a species may respond to climatic change in future scenarios can be substantively elevated.

Forest insects have a significant impact on ecological communities and their structure (Alfaro et al. 1999). Climate-insect relationships and historical outbreaks have been extensively explored in some ecosystems such as Vancouver Island and central BC (Kinghorn 1954; Alfaro et al. 1999); however, they are poorly understood in the ITR. Establishing the climate drivers and historic periodicity of WHL outbreaks in the ITR will enable forest managers to better anticipate the potential direct effects of climate change on growth and climate-mediated disturbance by WHL.

CHAPTER 3. SENSITIVITY OF WESTERN REDCEDAR TO CLIMATE IN BRITISH COLUMBIA'S INLAND TEMPERATE RAINFOREST

3.1 Introduction

3.1.1 Western Redcedar

Western redcedar is the dominant species in the ITR. It is widely distributed throughout coastal and wet inland forests of BC. It is a tall (maximum height approximately 60 m), scaly leaved evergreen tree (Klinka & Brisco 2009). Western redcedar-dominated stands are often driven by gap dynamics, and its shade tolerance allows for a slow canopy recruitment rate in a patchy form on the landscape (Kayahara et al. 1997; Klinka & Brisco 2009). It has a wide edaphic amplitude, but is most productive on fresh to moist nutrient-rich soils (Klinka & Brisco 2009). In the drier portions of the interior, western redcedar persists in fire–dominated seral ecosystems as well as very wet, cold ecosystems in the northern interior of its range (Jull et al. 1998; Arsenault & Goward 2000; Stevenson et al. 2011). This tree species has great economic, cultural, and ecological values and is considered the "flagship" species of the inland temperate rainforest.

3.1.2 Dendroclimatology

The growth of western redcedar in response to climate is well described in coastal BC (Kayahara et al. 1997; Klinka & Brisco 2009), but has not been well studied in the ITR. Stan and Daniels (2010) used tree-ring analysis to study the response of coastal western redcedar to climate variables and growth release from fine-scale disturbances. Dendroclimatology is a

large sub-branch of dendrochronology that encompasses analyses of tree-climate relationships, and reconstruction of past climate variables. Annual radial growth of trees reflect the variability of environmental factors that limit their growth (Fritts 1976; Fritts et al. 1991). When compared to climate data, tree rings can provide insight into the climate variables that are most limiting to growth, and have the most predictive power for a study species (Speer 2010). Correlation analysis is an accepted method of screening multiple climate variables to assess which are most important for a study species in a particular location (Fritts 1976). Response function analysis is a regression technique commonly used when examining climate variables and their effects on a given study species (Fritts & Xiangding 1986). This analysis is commonly carried out for the same variable combinations used for development of correlation matrices, in order to only report the combinations found to be significant (α=0.05).

3.1.3 Research Objectives

The purpose of this research is to examine the relationships between climate and western redcedar growth at different aspects and elevations within the ITR, using dendrochronological techniques and correlation analysis. The specific objective of the study is to identify trends and differences in significant climate-growth relationships for north- and south-facing slopes, and at elevations ranging from 667 m to 1240 m, the lower and upper ranges of the ITR in the study area.

3.2 Research Methods

3.2.1 Study Area

The study area was within the Interior Cedar Hemlock very wet, cool (ICHvk2) biogeoclimatic ecosystem classification (BEC) variant (Ketcheson et al. 1991), and was located approximately 100 km east of Prince George BC (Figure 3-1). Site selection was determined by computer based mapping using the Geographical Information System (GIS) ArcGIS 9.3 (Environmental Systems Research Institute 2010). A base layer of the ICHvk2 BEC variant located within the Prince George Forest District was created, then the Vegetation Resource Inventory (BCMOFR 2010) was overlaid on the study area and polygons that were identified as western redcedar leading were selected. If the canopy appeared, upon site visit, to be dominated by western redcedar by basal area or canopy closure then it was considered to meet this criterion. Shapefiles containing digitized air sketched maps of historical western hemlock looper outbreaks were downloaded from the Forest Insect and Disease Survey (FIDS) (Available at http://cfs.nrcan.gc.ca/publications/?id=19681) for the 1950s and 1990s outbreaks. All of these layers were clipped along the boundary of the ICHvk2 layer and then subsequently merged into one layer, effectively losing information about individual outbreaks and creating a layer that encompassed any stand that was affected by one or both of the known western hemlock looper outbreaks that occurred during the 20th century, and was also western redcedar leading. The resultant layer of candidate polygons met the following criteria: stands existed in the ICHvk2 BEC variant within the Prince George Forest District, were western

redcedar leading, and had been affected by western hemlock looper during one or both of the last two known outbreaks. In order to randomly select study sites, a "random points" layer was generated, with the criteria that points were no more than 500 metres from a road for ease of access, and that randomly generated points were at least 500 meters apart.

In order to determine if the sensitivity of western redcedar to climate variables changed with elevation or aspect, and to examine the spatial distribution of western hemlock looper outbreaks as part of a separate study, sampling was done at paired sites, one upper elevation and one lower elevation. At least one site in each pair was located in a known outbreak area. Six paired sites were sampled; three facing south and three facing north. All sites were located in the Robson River valley within the ICHvk2 variant, with the exception of one pair (two sites) located in the Torpy River valley, this due to limited road access in the Robson valley. Both valleys run roughly east-west, therefore each pair of sites had an approximate north- or south-facing aspect. The first pair of sites was located in the Lunate Creek Research Area to facilitate early season access, and because the area was part of the known western hemlock looper outbreak history. All other paired sites were selected using the random points layer to select the first site that met the access criteria. The paired site was located either up or down slope at a bearing perpendicular to the contour.

Once the potential sample areas had been identified and mapped, well-spaced paired sites were visually selected within patches of known WHL. These sites were verified as dominated by western redcedar by a walk-through survey. The final location of most paired sites changed slightly based on reconnaissance in order to target the oldest patches of trees within a polygon, reducing slightly the randomizing effect of computer-generated site spacing. On the north side of the valley, lower sites of the pair were established first with

corresponding upper sites located at the upper elevational limit of the cedar; on the south side of the valley upper elevation sites were established first then corresponding lower elevation sites were located at the lower elevation limits of western redcedar. In addition to these 12 sites, an additional site was selected; a level and well-drained western redcedar site within the historic outbreak area to minimize the effect of soil moisture on radial growth. In total, thirteen sites were sampled (See Figure 3-1).

3.2.2 Tree Ring Sampling

Twenty trees were sampled at each site, and large trees most likely to have the longest ring series were targeted. Trees were in the dominant canopy layer at each site. Sample trees were selected by coring the largest trees closest to the centre of the site until 20 trees had been sampled. Trees with very extensive heart-rot and therefore few growth rings remaining were not sampled. All sampling was completed between 2009 and 2011. Trees were sampled using an increment borer, and when possible, samples were taken at 0.3 metres from the ground. However due to the extensive heart rot typical of inland western redcedar; samples were taken from variable locations on the lower stem of the tree to collect a sample with minimal rot. In order to control for the incidence of locally absent rings, two samples were taken from each tree at opposing sides. Full cross-sections (discs) of dead and down trees were taken opportunistically using a chainsaw. The total number of cores that were analyzed was approximately 560, with approximately 35 discs processed.

3.2.3 Site sampling

Three sub-plots were established at each site to record species composition. Sub-plots were 7.89 m radius (0.2 ha), and were spaced 50 m apart with the first plot located at the first tree sampled at the site. Plots were oriented parallel with the slope contour. At each plot, the percent slope and aspect were recorded, and elevation was determined using a hand held Global Positioning System (GPS) unit, and subsequently plotted on a study map (Figure 3.1). Slope position was also recorded as lower (toe slope), mid-upper (mid slope), or upper (up slope).

The site series, based on *A field guide to site identification and interpretation for the southeast portion of the Prince George Forest Region* (DeLong 2003), was determined at each of the plots. Indicator species were used to determine plant associations that indicate relative soil moisture and nutrient status. Species composition was determined at each plot by recording the number of trees in each species in each of three strata: seedlings (trees equal or greater than 10 centimetres (cm) in height but less than or equal to 1.3 m in height), saplings (trees greater than 1.3 m in height but less than 7.5 cm in diameter), and canopy trees (trees greater than or equal to 7.5 cm in diameter). Table 3-2 is a composite basal area (m^2 per hectare) of both live and dead trees of all strata (canopy, sub-canopy, and saplings) based on the three 7.98 m radial plots measured at each site. Deciduous species were not counted in this stratum.

3.2.4 Sample Processing and Analysis

Cores were glued into wooden mounts, with the radial view facing upward. Cores were sanded down with progressively finer grits (Stokes & Smiley 1968). Annual rings of

each series were then assigned a calendar year by visual cross-dating using the list method (Yamaguchi 1991), then each ring in the series was measured to the nearest 0.001 millimetres using the Velmex "TA" System (Velmex, Inc. 1992) in conjunction with Measure J2X (Voor-Tech Consulting 2004). Visual cross-dating was verified using the computer program COFECHA (Holmes 1983) which performs a statistical comparison of lagged series (Speer 2010).

Cross-dated tree-ring series for each site were standardized using the program ARSTAN in interactive mode (Cook and Holmes 1984) to produce a standardized master chronology for each site. A rigid cubic smoothing spline of 66% series length frequency response with a 50% n cut-off was selected for de-trending each tree-ring series. The use of a rigid spline to remove long-term variation in ring width is a common standardization method (Speer 2010), but can result in lack of detection of shorter term variation (Peterson & Peterson 1994). The spline was fit to each observed ring-width series, and the observed ring widths were divided by the expected value to yield an indexed series. Individual growth indices were averaged together to create each site chronology. ARSTAN produces three versions of each standardized master chronology. The "standard chronology" includes inter-annual auto-correlation, or the influence of events in the previous year on ring width in the current year. The "residual chronology" has autocorrelation removed, and the "arstan chronology" includes modelled stand-level autocorrelation. The residual chronology was used for the following climate analyses. A small amount of individual samples yielded errors in the interactive version of ARSTAN, and these samples were treated with a more flexible spline length (33% of series length) in order for them to be incorporated into the overall chronology for further analysis.

3.2.5 Climate Data

Climate data were from the National Climate Data and Information Archive website (Environment Canada 2012) (http://climate.weatheroffice.gc.ca/Welcome_e.html). The National Climate Data and Information Archive is a federally managed collection of data from throughout Canada from various provincially and federally operated weather stations. In the case of this study, homogenized and raw weather data from the Prince George A weather station (Station ID 1096450, 53.9° N, 122.7° W) was used. Homogenized data have been cleaned by inserting interpolated values where data were missing, resulting in a complete average monthly record of maximum, minimum, and mean daily temperatures and averaged total monthly precipitation as rain, snow, and summed total daily precipitation. The data encompass the period from 1918 – 2009. All formats of temperature and precipitation data, including annual and seasonal averages, were derived from these values. Monthly values for the Pacific Decadal Oscillation (PDO) (Mantua & Hare 2002) were obtained from Nate Mantua's website (http://jisao.washington.edu/pdo/) (1900-2009) (Mantua 2010), and annual PDO values were obtained from Kaplan et al. (2000) (1854-1992). Monthly PDO values were derived from measured sea surface temperatures (Mantua 2010), and annual PDO values were extrapolated using tree ring data (Kaplan et al. 2000). Monthly growing degree days were calculated from temperature values from the Prince George A weather station by subtracting a base temperature of 10°C from the average daily temperature, then tallying the values over each month.

The program DendroClim2002 (Biondi & Waikul 2004) was used to examine the relationship between cedar radial growth and local climate variables. The climate variables

explored were average monthly minimum, maximum, and mean temperature, total precipitation as snow, total rain, and all precipitation, as well as monthly PDO and growing degree days (GDD). DendroClim2002 computes correlations between tree-ring indices and climate data and performs a response function analysis that uses principal components of monthly climate data and regression analysis (Fritts 1976). The window of analysis used was the May of the previous year to October of the current year ring formation for all tree ring and climate variable combinations. All sites (13 western redcedar chronologies in total) and climate variable combinations were sequentially analyzed for their significant correlation coefficients. Simple correlation coefficients were also computed between standardized chronologies and annually summed growing degree days, seasonally averaged temperature and precipitation, and annual total precipitation and mean temperature using the statistical package STATA (Statacorp 2012). Seasons were defined as follows: spring was March, April and May; summer was June, July, and August; fall was September, October, and November; and winter was December, January, and February. For all correlation computations, both the previous and present year climate data were run against standardized chronologies. All correlations were parametric and used Pearson's correlation coefficient. The PDO and GDD were explored for potential correlation with western redcedar growth using simple linear correlation. Annual PDO and GDD values were run against standardized chronologies for both previous and present year ring-width chronologies. Once the significant climate variables associated with tree growth for each site were identified, comparisons among sites were made to assess similarities and differences in climate drivers of tree growth.

In order to assess potential differences in tree growth among aspects, the climate variables mean annual precipitation and mean annual temperature were computed for each

site's geographic location using the software ClimateBC (Spittlehouse 2006a), using 1961 – 1990 normals. Sites were grouped based on aspect, and the resultant values were analyzed for differences between aspects using a t-test.

3.3 Results

3.3.1 Site Summaries

On the south side of the valley (north-facing aspect) the elevation of sample sites ranged from 682 m - 756 m for the low sites, and 1006 m to 1139 m for the higher elevation sites. On the north side of the valley (south-facing aspect) the elevation of sample sites ranged from 667 m - 820 m for the low sites, and 916 m to 1240 m for the higher elevation sites. Slopes were generally steeper on the north-facing aspects than on south-facing aspects. The most common site associations were the mesic *western redcedar/western hemlock – devil's club - lady fern* and sub-mesic *western redcedar/western hemlock – oak fern* communities (ICHvk2/01 and ICHvk2/04, respectively) (DeLong 2003). Mean DBH of western redcedar sampled for ring width measurements was 71.6cm. Species composition at each site is presented in tables 3-2 and 3-3. Sites were largely dominated by western redcedar, with western hemlock, spruce and subalpine fir often present in the canopy/sub-canopy and as saplings (Tables 3-2 and 3-3). Douglas-fir and deciduous trees were sparsely represented throughout the study sites. The most common seedlings in the understory were western redcedar, followed by western hemlock and sub-alpine fir. Spruce comprised a small portion of the seedlings, while no Douglas-fir seedlings were found (Table 3-3).

3.3.2 Chronologies

Tree-ring series that were cross-dated well within sites had series inter-correlations ranging from 0.56 to 0.65 and mean sensitivities above 0.2 (Table 3-1). The majority of chronologies began in the early 1700s, with some reaching into the 1600s, and the longest chronology into the late 1500s. The prevalence of heart-rot prevented the collection of longer time series. Decay was usually quite extensive, with considerable empty space between the innermost complete ring collected and the geometrical centre of the tree at coring height. Standardized chronologies displayed variation typical of climatic influence (i.e. high inter-annual variation). Figure 3.2 is an example of the residual chronology (Site 1) once standardized for use in climate analysis.

3.3.3 Climate – Growth Relationships

The correlation and response function analyses produced similar results in the direction (positive or negative) and magnitude of relationships between climate variables and ring width. For simplicity only the correlation coefficients are provided, but the reported relationships were limited to those that were statistically significant in both the bootstrapped correlation and response function analysis (Tables 3-4 to Table 3-10). Consistent positive correlations with sites between minimum, mean and maximum temperatures and tree growth were detected for the previous November and current January (Tables 3-4 to 3-6) (e.g. warm winters cause wide rings). Negative correlations with sites between mean and maximum monthly temperature and tree growth were detected for the current June (e.g. warm summers cause narrow rings). The most significant relationships were with maximum daily temperature (Table 3-6). With the exception of one site (site 5), tree growth at all upper elevation sites was

not sensitive to maximum June temperatures (Table 3-6), while all lower elevation sites were negatively correlated with maximum June temperatures (Table 3-6).

Correlation analyses between tree growth and total monthly precipitation yielded significant associations with a number of months, but no strong pattern (Tables 3-7 – 3-9). Previous November total precipitation was negatively correlated with tree growth at several sites, and current year March, May and October precipitation were positively correlated at numerous sites (Table 3-7). When the correlations with precipitation were limited to precipitation as snow, the negative correlations with the previous November were more consistent and correlation coefficients were higher (Table 3-8). Consistent positive correlations were found for precipitation as rain during the current year's growing season, especially spring and fall (Table 3.9). For both temperature and precipitation correlations, no differences in growth response emerged based on aspect; however growth responses to temperature did vary with elevation (Table 3-6) (related variables). Tree growth at high elevation sites was not sensitive to temperature, but tree growth was sensitive to temperature at low elevation sites.

Simple correlation analysis between annually averaged mean daily temperature (previous and current year), seasonally averaged mean daily temperature (previous winter to current summer), and tree ring growth (site) demonstrated that previous winter temperature was the only annual or seasonal temperature variable that was significantly correlated with tree growth. The relationship was positive and consistent across all sites. For precipitation, the only significant correlations were negative for current winter precipitation at sites 4, 7 and 9 – all of which were lower elevation sites.

Cumulative monthly growing degree days were significantly negatively correlated with tree growth, for June of the current growing season. A similar trend to that between

temperature and elevation was observed, with trees at upper elevation sites not as sensitive to growing degree days as trees at lower elevation sites, which showed consistent negative correlation between June growing degree days and ring width. No significant relationships were detected between previous and current year's total growing degree days, and ring width.

Correlation of tree growth with monthly values of the Pacific Decadal Oscillation produced only one significant result, at site 1 for current February. No significant relationships were found between tree ring growth and previous and current year's annual PDO values.

There were no significant differences between north and south-facing aspects for the variables mean annual precipitation (P=0.83) and mean annual temperature (P=0.07). Mean annual temperature and mean annual precipitation were both slightly higher on the south facing side of the valley (2.7°C, 1077.5 mm) than on the north-facing side of the valley (2.6°C, 848.5 mm).

3.4 Discussion

3.4.1 Sensitivity of Western Redcedar to Climate in the Inland Temperate Rainforest

Significant correlations between climate variables and tree growth were most commonly detected for monthly average temperatures and monthly total precipitation variables (monthly totals). Seasonally averaged or annual variables were not significantly correlated with tree growth (except mean winter temperature) which suggests that cedar growth is sensitive to climate at monthly, rather than seasonal or annual resolutions. Growing degree days in

June of the current year were consistently negatively correlated with tree growth. This relationship was consistent with the negative correlation of current June mean and maximum temperature with tree growth. Growing degree days are derived from temperature values, however we hypothesize more information about the relative importance of growing season length can potentially be derived from growing degree days in absence of specific data on growing season length in the study area.

Western redcedar growth in the study area is positively correlated with warm temperatures over the winter months, and negatively correlated with warm temperatures from late spring to early summer. Cold temperatures in the winter months may reduce the growing season length by delaying the snowmelt and reducing the biological activity near the soil into the following year's growing season. Soil microbial activity (linked to forest productivity) is known to be influenced by climatic factors such as precipitation and evapotranspiration (Brockett et al. 2012). The limiting effect of the previous winter temperatures on tree-growth is evidenced by positive correlations of tree growth with maximum daily temperatures in January of the current year. An alternate explanation is that warm January temperatures reduce snowpack and cause dry summer conditions (Table 3-6).

Western redcedar is known to be more tolerant of exogenous influences such as defoliating insects in warmer climates (Gregory 1957). Given this, it may explain the positive growth relationship this study has identified with warm winters if trees can build up more reserves under warmer conditions through extended beneficial growth conditions conducive to starch storage (Chapin III et al. 1990). During the summer months, increased temperatures may increase evapotranspiration in western redcedar growing in the ITR such that it becomes growth-limiting. The temperature sensitivity detected in this study is similar to that found by

Stan and Daniels (2010), who found that coastal western redcedar growth was negatively correlated with the previous year's July temperature. Differing adaptations (e.g. the importance of starch storage) of southern coastal versus northern interior western redcedar may explain why Stan and Daniels (2004) found negative correlations with temperature in the previous July on the south coast, while this study found negative correlations with temperature in June of the current year in the northern interior.

Western redcedar growth in the study area is negatively correlated with precipitation as snow in the early winter (November), and positively correlated with precipitation as rain throughout the growing season, especially in the current year March, May, and October (although the trees are most likely not responding to growing conditions at this point in the season). Precipitation as snow was the most strongly correlated with tree growth, compared to total precipitation and precipitation as rain, which were the 2nd and 3rd most strongly correlated. Increased precipitation as snow in November may precede long snowy winters with extensive snowpack persisting into the growing season. These long snowy winters, perhaps also in tandem with cold January temperatures, may limit the growing season of western redcedar through persistent snowpack and the resulting cold soils, known to limit activity of soil biota (Brockett et al. 2012) and water uptake, which in turn limits growth. The negative correlation with the previous November's snowpack contradicts other studies which state that an abundant snowpack is important for the growth of western redcedar in the inland temperate rainforest (Arsenault & Goward 2000; Stevenson et al. 2011). However, both of those studies also state precipitation is important to growth during the growing season, a result supported by this study (Table 3-7). Winter precipitation was not significantly correlated with tree-growth, which indicates a more specific connection with November snowpack than overall

snow accumulation. Positive growth relationships with total precipitation in March and May indicate the importance of growing season precipitation. Previous publications stating that western redcedar growth may be dependent on dense snowpack were not based on dendrochronological analysis, but rather observing dominant conditions in the ITR as a way of explaining the presence of species. Precipitation during the growing season is positively correlated with western redcedar growth, which was an anticipated result due to western redcedar's high moisture requirements (Klinka and Brisco 2009). Stan and Daniels (2010) found that growth is positively correlated with August precipitation for coastal western redcedar.

Previous year winter temperatures were significantly positively correlated with tree ring growth across all sites, and no other significant correlations with seasonal temperature variables were detected. Annual temperature (both current and previous year) yielded no significant correlations with tree ring width. This lack of sensitivity to annual temperature is important, given that western redcedar is known to experience growth increases from warmer climates on the Alaskan coast (Gregory 1957). This indicates differing adapted traits in interior western redcedar, potentially being more influenced by successive annual conditions than just the single previous year. Positive correlations with previous year January temperature found in this study are congruent with other western redcedar research done in other regions, finding positive correlations with previous winter temperatures through correlation analyses (Gregory 1957; Klinka & Brisco 2009).

Precipitation, when analyzed seasonally, yielded significant positive correlations with only three sites between tree ring growth and current year winter (all at lower elevation), and none for any other variable combinations. In addition, no significant correlations were detected between annual precipitation (previous and current year) and tree growth. This lack of

statistical sensitivity to seasonal or annual precipitation is also difficult to explain, given that other research has shown western redcedar to be sensitive to precipitation (Kayahara et al. 1997; Klinka and Brisco 2009;), but this may be due to a greater sensitivity to climate variables at the monthly scale. In addition there may be more appropriate seasonal monthly groupings for the study area. A possible explanation for the lack of sensitivity to seasonal climate fluctuations is the mild conditions in the ITR or ample groundwater flow (Stevenson et al. 2011) during the summer, which reduces stress on trees, as opposed to the pronounced drought experienced by coastal forests (Kayahara et al. 1997; Klinka & Brisco 2009). The positive current winter precipitation correlations (when analyzed seasonally) appear to contradict the results for monthly precipitation (negative correlations) in November (when analyzed monthly). One possible explanation is that the precipitation, although occurring in the winter, was actually rain, which was positively correlated with western redcedar growth in this study. The climate station in Prince George is approximately 100 km from the study area; therefore precipitation recorded as snow in Prince George could actually have been rain in the study area that study trees may have converted to growth.

Growing degree days, when analyzed monthly, were significantly correlated with tree ring growth in the current year June, and two sites were positively correlated between current year January and tree ring growth. The negative correlations in June mirror those of temperature, most likely due to the fact that growing degree days is highly dependent on the temperature available each day for biological activity to occur. When annual growing degree days were compared with tree ring growth, no significant correlations with tree growth were discovered for the current or previous year values, pointing to an elevated importance of monthly temperature rather than overall temperature during the growing season. The negative cur-

rent June temperature correlations with tree growth were most likely due to the fact that increased numbers of growing degree days means elevated daily temperatures in the summer months that may increase evapotranspiration in western redcedar growing in the ITR such that it becomes growth-limiting. Growing degree days as a variable is closely correlated with temperature, which limits is usefulness in modeling tree growth as a function of climate variables.

3.4.2 Effect of Aspect, Elevation, and Slope Position on Sensitivity to Climate

Aspect did not have an effect on sensitivity of tree-ring growth to any of the climate variables discussed above. Further, there was no difference in site series (identified by site and soil conditions and the vegetation community) between north- and south-facing aspects. Trees on both sides of the valley in the study area responded similarly to climate variables, and had similar plant associations and site conditions. It may be that differences in temperature and precipitation variables between the two aspects were not significant enough to change the relative sensitivity of western redcedar to these variables. Western redcedar has been shown to be shade tolerant (indicating a tolerance of low light availability) by other research, but only moderately tolerant to water deficit and heat, (Kayahara et al. 1997; Klinka & Brisco 2009) which might explain both the lack of sensitivity of western redcedar to solar orientation, and negative correlation with low moisture conditions during the summer months.

Low elevation sites were consistently located in the toe slope position, and high elevation sites in the upper slope position, so only elevation will be discussed further. No clear trends in growth sensitivity, based on the COFECHA chronology, or site series could be

identified based on elevation, and sites exhibited similar plant communities at a variety of landscape positions. Temperature and precipitation were not significantly different based on aspect, which could lead to differences in tree growth; however no differences were identified. On the other hand, elevation did have an effect on tree sensitivity to maximum daily temperature (Table 3-6). All low elevation sites displayed sensitivity (negative relationship) to both maximum temperature and growing degree days in current year June. Conversely, upper elevation sites (with the exception of one site) displayed a lack of sensitivity to both temperature and growing degree days in current year June. The single upper elevation site (site 5) displaying sensitivity to these variables was both drier (as indicated by the site series in Table 3-1), and the trees were smaller (Table 3-1), which may explain why those trees responded differently to temperature. This difference at the elevation level may be explained by the importance of growing season climate variables; upper elevation sites may be buffered from moisture stress by cooler temperatures and an ample supply of snowmelt, while lower elevation sites are subjected to higher temperatures. Other research has indicated an importance of moisture deficits (which varies on an elevational gradient) to western redcedar growth (Kayahara et al. 1997). Lower elevation sites may be more sensitive to temperature increases due to the microclimate at the valley bottom; warmer air masses may stay low and make warm days with high moisture stress even more intense due to the topographic position, driving soil processes that increase moisture stress in trees (Griffiths et al. 2009), while upper elevation trees experience milder conditions. High elevation sites may be buffered from increased moisture stress by cooler temperatures persisting at the higher elevations.

3.4.3 Conclusions and Future Climate Change Implications

Future climate change implications for western redcedar in the study area are a matter of ecological trade-offs. The two main climate results are negative correlations with increased previous winter snow and increased current summer temperatures (unique to lower elevation sites), and positive correlations with increased previous winter temperatures and increased current growing season precipitation as rain. If current climate change models are accurate, which predict warmer and wetter winters followed by dryer and warmer summers than presently observed (Hamann & Wang 2005), then the trade-offs based on western redcedar's tolerance for either harsh winters or stressful summers will determine any changes to future stand composition. If western redcedar's tolerance of warm and dry summers exceeds that of the tolerance for harsh winters, future climate change based on existing scenarios may be beneficial to growth due to a minimizing of the negative pressures from winter conditions combined with a lack of sensitivity to negative climatic conditions (i.e. warm summers) during the growing season. Conversely, if western redcedar's tolerance of harsh winters does not exceed that of the tolerance for warm and dry summers, stands may be negatively affected by the increased climatic pressure during the growing season despite the more favorable conditions during the winter. Stands growing at higher elevations are unlikely to be affected by the change in climatic regime due to their current insensitivity to warm summers, and stand to benefit from a changing climate of warmer, wetter winters. However those stands may become sensitive as temperature increases. Stands growing at lower elevations, however, may be affected adversely by climatic change, depending on the relative effect of each changing variable. Based on a future assumption of warmer and wetter winters, the most likely scenar-

ios are a positive growth trend for upper elevation stands and a negative growth trend for lower elevation stands.

Conclusions from this study are limited spatially to the study area (the ICHvk2 biogeoclimatic zone in the Prince George Forest District), but findings may be applied to other interior cedar hemlock ecosystems for management purposes. The majority of climate-growth relationships were based on pair-wise comparison of chronologies and climate data that spanned about 90 years, or in some cases longer. Overall, confidence in findings can be considered high because of the sample depth of both time and trees (n=272 trees). Site level correlations had significantly smaller sample depth (n=20 trees), however confidence can still be considered high due to consistent findings across many sites for several climate variables (i.e. maximum daily temperature, precipitation as snow, and total precipitation).

Table 3-1. Summary of site characteristics and summary statistics for all cross-dated sites (output from COFECHA).

Site	Aspect	Elevation(m) and Category	Site Series	Slope %	Sample Size (n)	Mean DBH	Timespan	Mean Sensitivity	Series Inter-correlation
1	N	1019 – High	ICHvk2/01	34	28	110.5	1711-2009	0.251	0.636
2	N	756 – Low	ICHvk2/04	5	21	72.0	1707-2009	0.231	0.607
3	N	1139 – High	ICHvk2/01	51	20	79.6	1717-2009	0.205	0.647
4	N	738 – Low	ICHvk2/01[05]	27	23	70.8	1760-2009	0.243	0.602
5	N	1006 – High	ICHvk2/02[03]	87	20	31.6	1867-2009	0.203	0.558
6	N	682 – Low	ICHvk2/04	0	20	60.8	1755-2009	0.235	0.584
7	S	667 – Low	ICHvk2/04	0	20	53.6	1694-2009	0.270	0.598
8	S	916 – High	ICHvk2/01	75	20	78.8	1650-2009	0.265	0.571
9	S	683 – Low	ICHvk2/01	0	20	64.2	1795-2009	0.275	0.581
10	S	1005 – High	ICHvk2/05[01]	14	21	97.4	1719-2009	0.206	0.607
11	S	820 – Low	ICHvk2/01[04]	10	15	61.8	1767-2009	0.272	0.581
12	S	1240 – High	ICHvk2/01	10	20	75.4	1777-2009	0.255	0.641
13	-	802 - Low	ICHvk2/04[03]	0	24	68.5	1595-2009	0.256	0.600

Notes: The following are descriptions of the Site Series found in Table 3-1. The ICHvk2/01: zonal western redcedar/western hemlock – devil's club – lady fern association, the ICHvk2/03: dry western hemlock/western redcedar – step moss association., the ICHvk2/04: mesic western redcedar/western hemlock – oak fern association, and the ICHvk2/05: wet western redcedar – devil's club – ostrich fern association.

Table 3-2. Basal area (m^2) of live and dead canopy/sub-canopy trees and saplings, by species, based on three 7.98 m radial plots at each site. Species are western hemlock (Hw), western redcedar (Cw), Spruce spp. (S), sub-alpine fir (Bl), Douglas-fir (Fd), and hardwood species (H).

Site	Aspect	Elevation (m)	Hw	Cw	S	Bl	Fd	H
1	N	1019 – High	0	17.1	<0.1	0	0	<0.1
2	N	756 – Low	1.2	2.3	0.2	0.8	0	0
3	N	1139 – High	0.9	8.7	0.2	0.5	0	0
4	N	738 – Low	1.3	8.2	0.4	0.3	0	0
5	N	1006 – High	0.2	1.1	0.3	0.1	1.6	<0.1
6	N	682 – Low	0.4	2.6	0.5	1.3	0	0.1
7	S	667 – Low	0	4.2	0.4	0.9	0	0.3
8	S	916 – High	1.1	12.0	<0.1	<0.1	0	0
9	S	683 – Low	<0.1	1.9	1.3	1.3	0	0.4
10	S	1005 – High	0.9	5.6	0.8	0.3	0	0.1
11	S	820 – Low	1.0	1.5	0.8	0.3	0	0.1
12	S	1240 – High	1.2	8.3	0.5	0.2	0	0
13	-	802 - Low	1.6	3.0	<0.1	0.4	0	0

Table 3-3. Seedling tally by species and site.

Site	Aspect	Elevation (m)	Hw	Cw	S	Bl
1	N	1019	0	5	16	0
2	N	756	76	64	1	2
3	N	1139	1	3	0	1
4	N	738	0	30	0	10
5	N	1006	6	67	0	1
6	N	682	10	53	0	27
7	S	667	0	100	0	8
8	S	916	13	4	0	0
9	S	683	0	29	4	39
10	S	1005	27	19	2	2
11	S	820	37	27	7	3
12	S	1240	0	3	1	0
13	-	802	53	13	0	7

Table 3-4. Correlation

values for significant ($\alpha = 0.05$) relationships (1920-2009) between ring width (site) and monthly average minimum temperature, from the previous May (M) to October (o) of the year of ring formation.

			Months relative to ring formation																	
Site	Aspect	Elevation (m)	M	J	J	A	S	O	N	D	j	f	m	a	m	j	j	a	s	o
1	N	1019	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	N	756	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	N	1139	-	-	-	-	-	-	0.334	-	-	-	-	-	-	-	-	-	-	-
4	N	738	-	-	-	-	-	-	0.283	-	0.309	-	-	-	-	-	-	-	-	-
5	N	1006	-	-	-	-	-	-	0.257	-	-	-	-	-	-	-	-	-	-	-
6	N	682	-	-	-	-	-	-	-	-	0.329	-	-	-	-	-	-	-	-	-
7	S	667	-	-	-	-	-	-	-	-	0.297	-	-	-	-	-	-	-	-	-
8	S	916	-	-	-	-	-	-	-	-	0.330	0.323	-	-	-	-	-	-	-	-
9	S	683	-	-	-	-	-	-	-	-	0.241	-	-	-	-	-	-	-	-	-
10	S	1005	-	-	-	-	-	-	0.283	-	0.260	-	-	-	-	-	-	-	-	-
11	S	820	-	-	-	-	-	-	0.252	-	-	-	-	-	-	-	-	-	-	-
12	S	1240	-	-	-	-	-	-	0.239	-	-	0.275	-	-	-	-	-	-	-	-
13	-	802	-	-	-	-	-	-	0.265	-	0.236	-	-	-	-	-	-	-	-	-

Table 3-5. Correlation values for significant ($\alpha = 0.05$) relationships (1920-2009) between ring width (site) and mean daily temperature, by month, from the previous May (M) to October (o) of the year of ring formation.

Site	Aspect	Elevation (m)	Months relative to ring formation																	
			M	J	J	A	S	O	N	D	j	f	m	a	m	j	j	a	s	o
1	N	1019	-	-	-	-	-	-	-	-	0.226	-	-	-	-	-	-	-	-	-
2	N	756	-	-	-	0.297	-	-	-	-	-	-	-	-	-	-0.327	-	-	-	-
3	N	1139	-	-	-	0.234	-	-	0.327	-	-	-	-	-	-	-	-	-	-	-
4	N	738	-	-	-	-	-	-	0.263	-	0.329	-	-	-	-	-	-	-	-	-
5	N	1006	-	-	-	-	-	-	0.255	-	0.210	-	-	-	-	-0.271	-	-	-	-
6	N	682	-	-	-	-	-	-	-	-	0.351	-	-	-	-	-0.222	-	-	-	-
7	S	667	-	-	-	-	-	-	-	-	0.313	-	-	-	-	-0.233	-	-	-	-
8	S	916	-	-	-	-	-	-	-	-	0.343	0.316	-	-	-	-	-	-	-	-
9	S	683	-	-	-	-	-	-	-	-	0.256	-	-	-	-	-0.257	-	-	-	-
10	S	1005	-	-	-	-	-	-	0.273	-	0.287	-	-	-	-	-	-	-	-	-
11	S	820	-	-	-	-	-	-	0.244	-	0.229	-	-	-	-	-0.254	-	-	-	-
12	S	1240	-	-	-	-	-	-	0.231	-	-	0.284	-	-	-	-	-	-	-	-
13	-	802	-	-	-	-	-	-	0.259	-	0.259	-	-	-	-	-0.248	-	-	-	-

Table 3-6. Correlation values for significant ($\alpha = 0.05$) relationships (1920-2009) between ring width (site) and monthly average maximum temperature, from the previous May (M) to October (o) of the year of ring formation.

Site	Aspect	Elevation (m)	Months relative to ring formation																	
			M	J	J	A	S	O	N	D	j	f	m	a	m	j	j	a	s	o
1	N	1019	-	-	-	-	-	-	-	-	0.244	-	-	-	-	-	-	-	-	-
2	N	756	-	-	-	0.220	-	-	-	-	0.259	-	-	-	-	-0.396	-	-	-	-
3	N	1139	-	-	-	-	-	-	0.312	-	0.203	-	-	-	-	-	-	-	-	-
4	N	738	-	-	-	-	-	-	-	0.268	0.347	-	-	-	-	-0.251	-	-	-	-
5	N	1006	-	-	-	-	-	-	0.248	-	0.230	-	-	-	-0.267	-0.335	-	-	-	-
6	N	682	-	-	-	-	-	-	-	0.294	0.375	-	-	-	-	-0.270	-	-	-	-
7	S	667	-	-	-0.184	-	-	-	-	-	0.328	-	-	-	-	-0.282	-	-	-	-
8	S	916	-	-	-	-	-	-	-	-	0.356	-	-	-	-	-	-	-	-	-
9	S	683	-	-	-	-	-	-	-	-	0.273	-	-	-	-0.238	-0.325	-	-	-	-
10	S	1005	-	-	-0.203	-	-	-	0.262	-	0.316	-	-	-	-	-	-	-	-	-
11	S	820	-	-	-	-	-	-	0.232	-	0.257	-	-	-	-	-0.275	-	-	-	-
12	S	1240	-	-	-	-	-	-	-	-	0.207	0.276	-	-	-	-	-	-	-	-
13	-	802	-	-	-	-	-	-	0.246	-	0.288	-	-	-	-	-0.303	-	-	-	-

Table 3-7. Correlation values for significant ($\alpha = 0.05$) relationships (1918-2008) between ring width (site) and monthly average precipitation, from the previous May (M) to October (o) of the year of ring formation.

Site	Aspect	Elevation (m)	Months relative to ring formation																
			M	J	J	A	S	O	N	D	j	f	m	a	m	j	j	a	s	O
1	N	1019	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.227
2	N	756	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.348
3	N	1139	-	-	-	-	-	-	-0.265	-	-	-	-	-	-	-	-	-	-	-
4	N	738	-	-	-	-	-	-	-	-	-	-	0.388	-	-	-	-	-	-	0.388
5	N	1006	-	-	0.262	0.284	-	-	-0.279	-	-	-	-	-	0.312	-	-	-	-	-
6	N	682	-	-	-	-	-	-	-	-	-	-	0.291	-	-	-	-	-	-	0.286
7	S	667	-	-	-	-	-	-	-	-	-	-	0.405	-	-	-	-	-	-	0.301
8	S	916	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.249
9	S	683	-	-	-	-	-	-	-	-	-	-	0.236	-	0.406	-	-	-	-	0.339
10	S	1005	-	-	-	-	-	-	-0.199	-	-	-	-	-	-	-	-	-	-	-
11	S	820	-	-	-	-	-	-	-0.189	-	-	-	0.262	-	0.264	-	-	-	-	-
12	S	1240	-	-	-	-	-	-	-0.240	-	-	-	0.264	-	0.285	-	-	-	-	-
13	-	802	-	-	-	-	-	-	-0.212	-	-	-	-	-	0.356	-	-	-	-	-

Table 3-8. Correlation values for significant ($\alpha = 0.05$) relationships (1919-2008) between ring width (site) and total daily precipitation as snow, by month, from the previous May (M) to October (o) of the year of ring formation.

Site	Aspect	Elevation (m)	Months relative to ring formation																	
			M	J	J	A	S	O	N	D	j	f	m	a	m	j	j	a	s	O
1	N	1019	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	N	756	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.296
3	N	1139	-	-	-	-	-	-	-0.350	-	-	-	-	-	-	-	-	-	-	-
4	N	738	-	-	-	-	-	-	-0.249	-	-	-	-	-	-	-	-	-	-	-
5	N	1006	-	-	-	-	-	-	-0.295	-	-	-	-	-	-	-	-	-	-	-
6	N	682	-	-	-	-	-	-	-0.273	-	-	-	-	-	-	-	-	-	-	-
7	S	667	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	S	916	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	S	683	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	S	1005	-	-	-	-	-	-	-0.287	-	-	-	-	-	-	-	-	-	-	-
11	S	820	-	-	-	-	-	-	-0.270	-	-	-	-	-	-	-	-	-	-	-
12	S	1240	-	-	-	-	-	-	-0.258	-	-	-	0.208	-	-	-	-	-	-	-
13	-	802	-	-	-	-	-	-	-0.284	-	-	-	-	-	-	-	-	-	-	-

Table 3-9. Correlation values for significant ($\alpha = 0.05$) relationships (1919-2008) between ring width (site) and total daily precipitation as rain, by month, from the previous May (M) to October (o) of the year of ring formation.

Site	Aspect	Elevation (m)	Months relative to ring formation																
			M	J	J	A	S	O	N	D	j	f	m	a	m	j	j	a	s	o
1	N	1019	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	N	756	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.190
3	N	1139	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	N	738	-	-	-	-	-	-	-	-	-	-	0.320	-	0.390	-	-	-	-	0.297
5	N	1006	-	-	-	0.284	-	-	-	-	-	-	0.224	-	0.297	-	-	-	-	-
6	N	682	-	-	-	-	-	-	-	-	-	-	0.286	-	-	-	-	-	-	0.269
7	S	667	-	-	-	-	-	-	-	-	-	-	-	-	0.406	-	-	-	-	0.268
8	S	916	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	S	683	-	-	-	-	-	-	-	-	-	-	-	-	0.394	-	-	-	-	0.313
10	S	1005	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	S	820	-	-	-	-	-	-	-	-	-	-	-	-	0.255	-	-	-	-	-
12	S	1240	-	-	-	-	-	-	-	-	-	-	-	-	0.275	-	-	-	-	-
13	-	802	-	-	-	-	-	-	-	-	-	-	-	-	0.350	-	-	-	-	-

Table 3-10. Correlation values for significant ($\alpha = 0.05$) relationships (1914-2006) between tree growth (site) and daily growing degree days, by month, from the previous May (M) to October (o) of the year of ring formation.

Site	Aspect	Elevation (m)	Months relative to ring formation																	
			M	J	J	A	S	O	N	D	j	f	m	a	m	j	j	a	s	o
1	N	1019	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	N	756	-	-	-	-	-	-	-	-	0.323	-	-	-	-	-0.412	-	-	-	-
3	N	1139	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	N	738	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.240	-	-	-	-
5	N	1006	-	-	-	-	-	-	-	-	0.203	-	-	-	-	-0.314	-	-	-	-
6	N	682	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.282	-	-	-	-
7	S	667	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.294	-	-	-	-
8	S	916	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	S	683	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.372	-	-	-	-
10	S	1005	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	S	820	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.256	-	-	-	-
12	S	1240	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	-	802	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.340	-	-	-	-

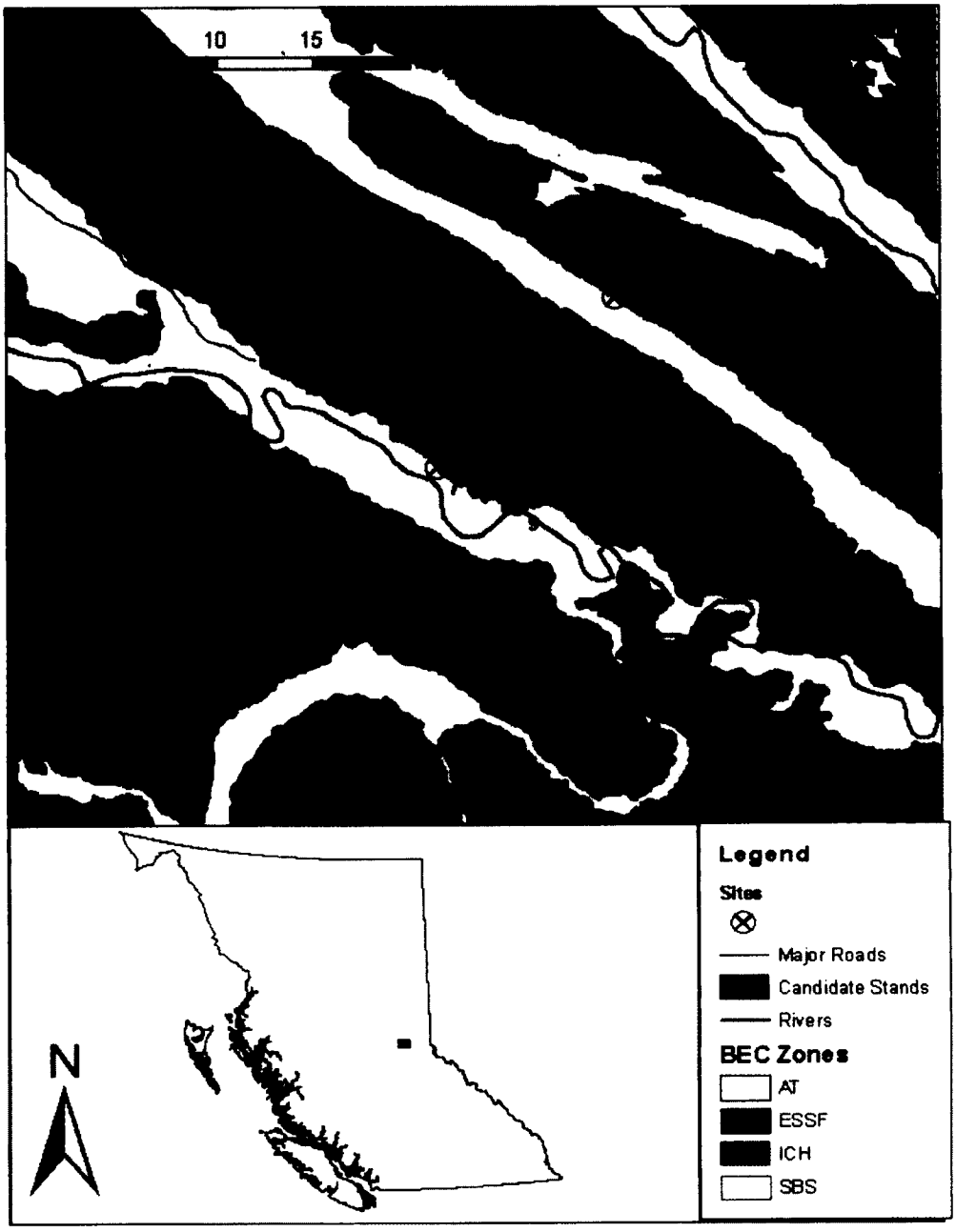

Figure 3.1. Map of study area and site locations.

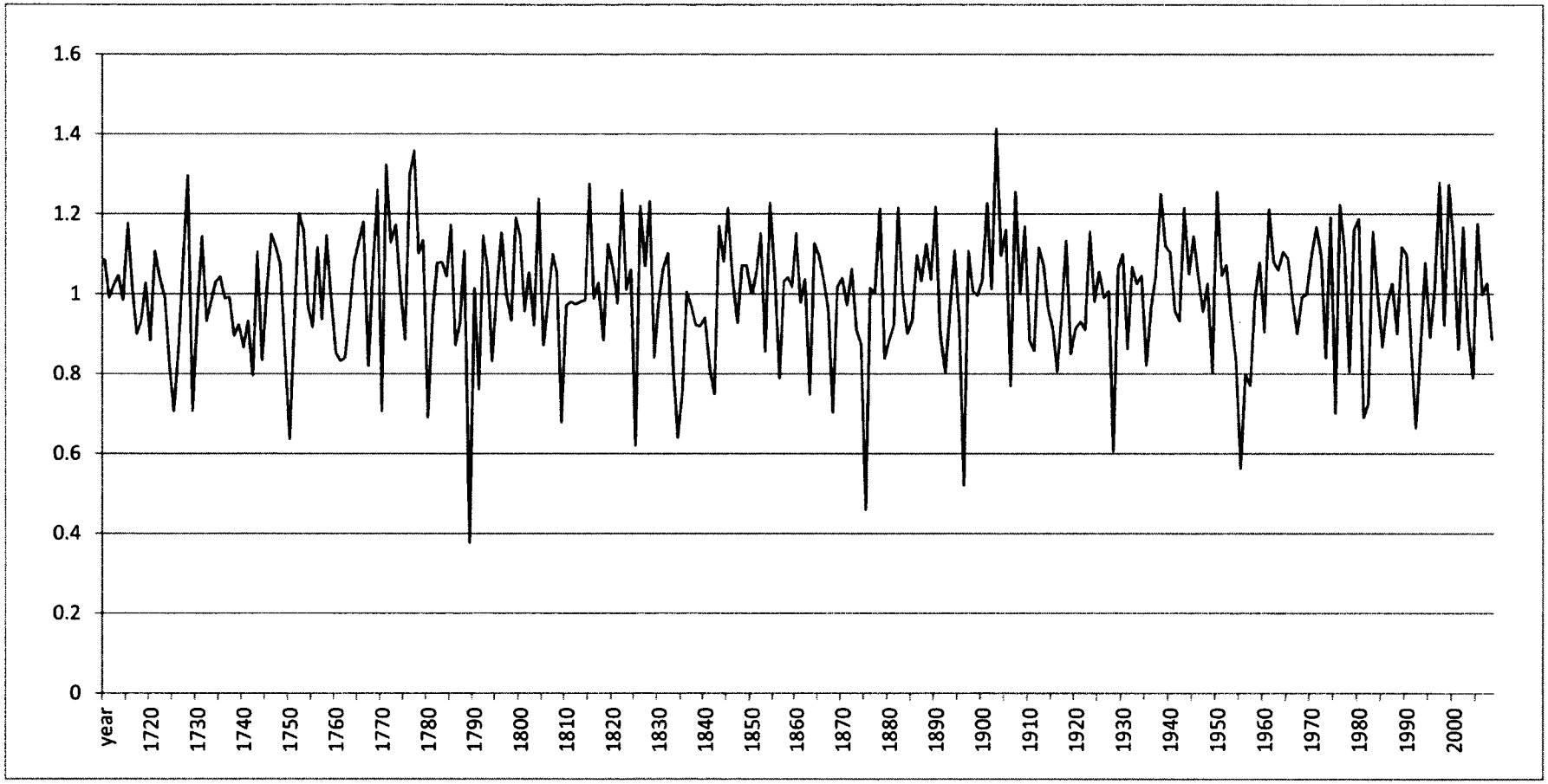

Figure 3.2. Site level chronology with calendar year on x-axis and standardized residual values for Site 1 on y-axis. Values are indexed, where 1 = the average value across all years.

CHAPTER 4. WESTERN HEMLOCK LOOPER IN THE INLAND TEMPERATE RAINFOREST

4.1 Introduction

4.1.1 Western Hemlock Looper and Disturbance

Western Hemlock Looper occurs in BC in most western hemlock dominated and co-dominated stands and is considered to be one of the most destructive forest insects in the province (Turnquist et al. 1995). Two historic outbreaks have occurred in the Interior Cedar Hemlock zone southeast of Prince George, BC. These were recorded and mapped by the Forest Insect and Disease Survey (FIDS). One outbreak occurred in 1954-1955 and defoliated 39,000 ha, and one outbreak occurred in 1992-1994 and defoliated 45,000 ha (Turnquist et al. 1995; Hoggett and Negrave 2002). WHL will defoliate all known tree species during an outbreak (Hoggett and Negrave 2002), but appears to defoliate spruce the least (Alfaro et al. 1999). Although often driven primarily by temporal population cycles, defoliators are known to be sensitive to climate, and in many cases population sizes are affected by variability in regional climate (Myers 1988). For example, WHL outbreaks have been shown to coincide with early summer moisture deficits in south coast BC (McCloskey 2007).

Disturbance is an important element in forest systems and influences stand age and composition (Delong 2007). Disturbance can be caused by biotic and abiotic agents, such as insect outbreaks and fire respectively, and can be at the landscape to small gap scale. Disturbance influences the regeneration dynamics in stands by causing mortality or

suppression in trees, subsequently regulating the available light, water, and nutrients (Alfaro et al. 1999). Trees respond to disturbance agents in various ways depending on the type of damage caused and how it influences normal physiological function. Defoliators such as WHL feed on the foliage of trees, reducing the tree's photosynthetic capacity. Trees then must use energy reserves to replace lost foliage. This requires energy, and combined with the reduced photosynthetic capacity during outbreak years, results in suppression of radial growth during and after outbreaks. This growth suppression has been used to reconstruct and quantify the frequency, severity, and other characteristics of insect outbreaks in temperate forests (Alfaro and MacDonald 1988, Bouchard et al. 2006).

4.1.2 Dendroentomology

Dendrochronology provides a well-accepted approach to studying outbreak dynamics of biotic disturbance agents, including defoliating insects and fungi, and their effects on stand dynamics (Swetnam and Lynch 1993). Tree-ring based studies of defoliating insects take advantage of the growth suppression effects caused by the defoliator, and compare growth rates of host species with those of a non-host species. The non-host chronology is also applied to reduce the influence of climate on the outbreak chronology (Alfaro et al. 1999; Thompson et al. 2007). One assumption of this approach is that both host and non-host species respond to climate similarly, and this is tested using correlation analysis and visual assessment. WHL is a generalist feeder, as it feeds on herbaceous species and many tree species (Thomson 1957). Therefore, application of the non-host comparison approach to develop outbreak chronologies for WHL is challenging as there is no true non-host species that can be reliably determined to have not been defoliated. However it is possible to find

nearby forest stands which due to modest differences in elevation, are outside the range for defoliation. Past studies have shown that the Engelmann spruce-subalpine fir BEC zone, just above the ICH in elevation, made up a small percentage of the areas defoliated during recorded outbreaks (Jull et al. 1998). Trees in these stands would be exposed to similar climate and local weather, but would be less likely to have been significantly defoliated by WHL compared to western redcedar. Further, spruce is one of the least preferred hosts for WHL and is less likely to be defoliated when other species are available (Alfaro et al. 1999).

4.1.3 Research Objectives

A large amount of uncertainty surrounds the future of the ITR. It has been shown that growth of trees in the Interior Cedar-Hemlock zone is positively correlated with the extensive snowpack and mild, humid summers that are typical to the ITR (Hebda 1995, 1997) (Chapter 3). However, little is known about future forest responses to changing climate, including responses to changes in WHL outbreak dynamics as a result of climate change. The purpose of this research was to quantify the outbreak dynamics of WHL on western redcedar in the ITR, and determine the influence of climate variables on outbreak dynamics. Specific objectives were to: 1) Identify a tree-ring signal in western redcedar that can be used to reconstruct historic outbreaks of WHL; 2) Quantify the WHL outbreak regime by outbreak frequency and severity; 3) Determine if differences exist in outbreak dynamics (i.e. frequency and severity) among different elevations and aspects; and 4) Identify climate variables that are important drivers of WHL outbreaks.

4.2 Research Methods

4.2.1 Site Selection and Sampling

Site selection and sampling are described in Chapter 3. At least one of two sites in each transect was located in an area of known WHL outbreak history, to the greatest extent possible. In order to achieve the objective of elevational transects, usually one site was not located in a known WHL outbreak location.

4.2.2 Western Hemlock Looper Analysis

All cross-dated series were standardized to a mean of one, using the program ARSTAN (Cook & Krusic 2011). Several deterministic and stochastic growth trends were tested, and a flexible smoothing spline of 33% of measured series length was chosen to retain low frequency events occurring at large temporal scales, based on the relatively short outbreak duration of WHL and the length of time between successive defoliation events. The spline was fit to each series, and the actual ring width was divided by the modeled curve value to produce a dimensionless index series which was used to detect WHL outbreaks in individual trees.

To reduce the influence of climate on each series, and to accentuate the growth reductions caused by WHL, an indexed ring-width chronology from a non-host (or less preferred host, as WHL has a very broad host range) species was subtracted from each host series. An Engelmann spruce chronology near the study area was used for this purpose (Thompson et al. 2007). Engelmann spruce can also be defoliated by WHL but the chronology site was not affected by either of the known outbreaks, and was suspected to be at

too high an elevation for significant damage due to WHL. The non-host species must have similar climate-growth responses as the host species (Ryerson et al. 2003), and this was assessed by graphical comparison and pairwise correlation analysis of the two species (Figure 4-2). Climate-growth relationships for the Engelmann spruce chronology and western redcedar were compared for the variables maximum daily temperature, total precipitation, and growing degree days. Analyzed visually and statistically, the Engelmann spruce chronology responded to climate similarly enough to western redcedar to warrant use in outbreak reconstruction. The spruce cores were examined for growth reduction during the known outbreak periods, but no reductions were observed. A corrected index series for each western redcedar series was calculated using the following equation:

Corrected index = Hc (i) = Hi (i) - (Ci (i) - Cmn) Hsd / Csd

Where Hc (i) is the corrected host index at year (i), Hi (i) is the host tree-growth index for year (i), Ci (i) is the control chronology index for year (i), Cmn is the control chronology mean in the common time span, Hsd is the host series standard deviation in the common time span and Csd is the control chronology standard deviation in the common time span (Holmes 1983). In all cases the length of the series and chronologies were truncated to the period held in common by both. This climate correction procedure is automated by the program OUTBREAK (Holmes and Swetnam 1996). Each host index series was corrected individually using the non-host chronology, and then resultant corrected series were averaged within each site to create a climate-corrected host chronology for each series. Normalized corrected series were summarized by site. Periods of negative corrected host index (where the host growth was less than non-host growth) that met specific user-identified criteria in OUTBREAK were identified as WHL outbreaks. The criteria applied in this study were

developed by comparing the timing and duration of the reductions in the corrected chronology with the pattern observed in the wood samples during periods of known outbreak. A characteristic pattern of growth suppression was identified, and from these an initial set of criteria were developed based on timing and duration of the ring-width reductions. The program was run iteratively until the two known outbreaks (known as the calibration period) were identified reliably with the outbreak criteria. Final criteria were: maximum growth reduction at least -1.85 standard deviations below the non-host species, suppression period between 5 and 8 years, growth reduction in the first year of an outbreak at least 1 standard deviation from the corrected host chronology. Control chronology index values greater than 1 were raised to the power of 0.3 in order to suppress the effects of large positive values, which may produce false positives in the identification of outbreaks. The program was run for all individual cedar series with the non-host spruce chronology, and then a site-level outbreak chronology was developed for each of the 13 western redcedar sites. In order for an apparent outbreak to be included in a site-level outbreak chronology, 10% of all trees in the site must have shown growth reductions that met the OUTBREAK criteria within three years from the inferred outbreak start. The 10% threshold was determined from the 1950s outbreak, which was evident in just over 10% of trees (Figure 4-4). Outbreak start years were estimated to be two years prior to the beginning of the most severe year of suppression (most trees recording an outbreak), based on observations from the two known outbreaks.

Superposed epoch analysis was used to examine the relationships between climate variables and onset/decline of WHL outbreaks. Superposed epoch analysis compares mean conditions of a response variable (in this case corrected ring width index), before, during and after an event, which is then superimposed on possible predictor variables. For the period

1920 to 2009 the start year of an outbreak was used as the event year and investigated current year conditions and those over an 11-year window, which included the 6 years preceding and the 4 years following the start of an event. This analysis has been commonly used to study fire-climate relationships (e.g. Hessl et al. 2004) and has been adopted for studies of insect-climate relationships (i.e. Pohl et al. 2006). I used the program EVENT (Holmes and Swetnam 1994) to carry out the analysis, which automates the comparison of each event window with 1000 randomly-selected event years to calculate boot-strapped confidence intervals. Departures of the actual from simulated observations were considered significant at the 95% level. I developed a moisture stress index using precipitation and temperature according to White (1969). A z-score was calculated by subtracting the average temperature across the dataset from the observed temperature, and the result was divided by the standard deviation of the temperature across the dataset. Then precipitation was treated in the same way. The value generated from precipitation was subtracted from the value generated from temperature, creating a moisture stress index. July temperature (June is known to be an important climatic month for WHL in BC's lower mainland, therefore July was used to adjust for the comparatively shorter growing season in the study area) (McCloskey et al. 2009) and July precipitation, and summer temperature (June, July, August) and summer precipitation were all used to create a moisture stress index for each variable combination. The resultant July and summer moisture stress indices were assessed for their relationship to outbreaks using the program EVENT (Holmes and Swetnam 1994). I then repeated this process using temperature only as a climate variable. Climatic differences with regards to aspect and elevation, t-test comparisons are described in Chapter 3. Outbreak severity and frequency were compared between high and low elevation sites, and between north- and south-facing

aspects, using t-tests. Sites were stratified by north and south, and high and low elevation to perform comparisons.

4.3 Results

Series inter-correlations ranged from 0.558 to 0.647, which indicated good cross-dating within sites. Table 3-1 summarizes cross-dating statistics and site variables. Species composition of canopy trees, sub-canopy trees and saplings are presented in Table 3-2, and seedlings in Table 3-3. Table 3-2 is a composite basal area of both live and dead trees of all strata based on the three plots at each site.

4.3.1 Outbreak Reconstruction

Standardized chronologies displayed variation typical of low frequency events such as western hemlock looper outbreaks. Figure 4-1 is an example of the standard chronology of an individual site (Site 1) once standardized for use in outbreak analysis. Visually assessed, the Engelmann spruce residual chronology that was used as a climate control for outbreak reconstruction shows similar high frequency variation in ring width index to that of western redcedar growing in the study area (Figure 4-2). The Engelmann spruce showed similar negative response to growing degree days, with correlation coefficients ranging from -0.2083 to -0.2768 (all $P=<0.05$), and late summer precipitation (0.3544, $P=<0.05$) as western redcedar (Chapter 3). It differed from western redcedar (which responded negatively to June temperature, Chapter 3), with a positive response to June mean temperature (0.2676, $P=<0.05$). How-

ever, the influence of climate on the results was limited by the method of standardization, and spruce did not display growth reduction during years in which WHL outbreaks were known to have occurred in the study area. Figure 4-3 shows all trees recording outbreaks from 1615 to 2009 for all sites, as well as the sample depth. Figure 4-4 shows the percent of trees recording outbreaks, at each point in time. Confidence in outbreak prediction decreases going back through time due to a decreasing sample size. Table 4-1 provides the number of trees at each site that recorded an outbreak where at least 10% of trees at that site recorded the outbreak. Known outbreaks beginning in 1992 and 1954 were identified from historical records as well as in the tree rings, and additional outbreaks were inferred for 1920, 1897, 1874, 1834, 1785, and 1741. Other periods of potential western hemlock looper-related suppression were detected earlier in the dataset, but sample size was too low to confidently call these suppression events outbreaks.

The mean return interval is 36 years for the 1900s, 31.5 years for the 1800s, and 44 years for the 1700s (only one interval). Figure 4-5 shows the variation in return interval over time by plotting the length of time from the preceding outbreak against the start date of the next outbreak. The return interval varied over time and showed no trends. The total mean return interval is 35.6 ± 9.5 years. Table 4-2 summarizes sites recording inferred outbreaks when compared to the control chronology as a mean site chronology, rather than individual series. Results from the t-tests showed that aspect had no significant effect on frequency ($P=0.8670$) or severity ($P=0.6007$) of outbreaks. Outbreaks at upper elevation sites were significantly more severe (based on number of trees recording an outbreak) than lower elevation sites ($P=0.0290$), but frequency was not different based on elevation ($P=0.3411$).

For the known outbreak periods, the majority of trees displayed suppression before the recorded start year according to survey data. For example, ring-widths in 1990 and 1991 are commonly suppressed yet the outbreak was identified to begin in 1992. Similarly, suppression beginning pre-1954 (in some cases for several years before) was common for that outbreak as well. The duration of suppression during outbreaks ranged from 3 – 8 years, with many trees continuing to exhibit suppression that met outbreak criteria up to five years post-outbreak period; in those cases the suppression began later than the inferred start date of that outbreak and met the criteria. Many trees experienced and survived multiple outbreaks throughout their lifetime, the most being one tree at site 8 (south facing, upper elevation) which recorded 8 outbreaks over its observed lifespan.

4.3.2 Superposed Epoch Analysis

Several climate variables were found to be significantly associated with outbreak timing. The July and summer (June, July, and August) moisture stress indices were significantly higher 2-3 years preceding the start of an outbreak although the year prior to the outbreak start was not significantly different from the mean (Figs. 4-6 and 4-7). Analysis with temperature variables showed that annual temperature was significant at the year of outbreak (Figure 4-8), and July (Figure 4-9) and summer temperature (Figure 4-10) were significant at the -3 year. Temperature, moisture stress, and precipitation are all likely auto-correlated as similar results from moisture stress and temperature SEAs indicate; yet temperature analyses showed some differences such as significance in the year of outbreak (Fig. 4-8). $P=<0.05$ for all significant SEA analyses.

4.4 Discussion

Known and apparent WHL outbreaks were identified through three centuries with varying degrees of severity and frequency of trees recording outbreaks at a given sample site, as well as in total. All sites contained trees recording at least one outbreak, and most sites contained at least one tree recording every reconstructed outbreak. Known outbreaks periods of 1954-1955 and 1992-1994 were identified, as well as additional outbreaks in the 1900s, three outbreaks in the 1800s and two in the 1700s. However sample size diminishes with increasing time since present, therefore there is less confidence in the accuracy of outbreak reconstruction during the earlier part of the outbreak chronology, especially prior to 1800 where the sample size is less than 10 trees.

4.4.1 Outbreak Reconstruction

For the known outbreak periods, the actual start of suppressed growth observed in the tree rings preceded the surveyed start date of the outbreak by several years. One possible explanation for this is that defoliation only becomes evident to an aerial surveyor after multiple years of defoliation. Error in estimating outbreak start years could have resulted in error in determination of climate drivers at the annual resolution during moisture stress SEA (skewing the results backwards in time and therefore identifying the -3 and -2 years as significant), but temperature SEA showed significance in the year of outbreak. Some trees also recorded suppression beginning in or around 1983, a known outbreak in the ITR outside of the study

area to the east. It is possible that a small number of trees in the study area experienced defoliation from that outbreak, although it was mapped as having occurred elsewhere.

A total of eight outbreak periods were identified. Throughout the 1900s there were three outbreaks; the two known outbreaks beginning in 1954 and 1992, as well as an outbreak in the 1920s which was within the calibration period, but had not been identified during ground-based surveys. Although the FIDS began in 1911, aerial surveys were not completed until the 1940s (Phil Burton, pers. comm. 2012), and the highway through the study area did not exist until 1964 (British Columbia Ministry of Transportation and Highways 2013), which would have limited access. It is likely that this outbreak was missed by surveyors due to the remoteness of the study area.

Climatic pressures such as moisture stresses may affect host vigor, and therefore the ability to mount defense responses or refoliate, as western redcedar thrives in moist, mild climates (Klinka & Brisco 2009). The same climatic variable which stressed western redcedar in the study, increased summer temperatures (see Chapter 3), contributes to elevated moisture stress which was found to precede WHL outbreaks in this study (Figure 4-6 to 4-10) and in a study from the lower mainland of British Columbia (McCloskey 2007; McCloskey et al. 2009). Defoliation by WHL on vigorous trees may not result in growth reduction, but trees stressed by climate and then subject to a WHL outbreak are likely to show growth suppression, and possibly even mortality (Kinghorn 1954; Turnquist et al. 1995; Alfaro et al. 1999). In this study upper elevation stands were more severely defoliated than lower elevation stands which is in line with Alfaro et al. (1999) who found that upper elevation stands in the same general study area were more severely defoliated and suffered greater mortality. Kinghorn (1954) found the opposite on Vancouver Island, where lower elevation stands were

more severely defoliated. Broad climatic differences between coastal BC and the ITR such as colder winters (Stevenson et al. 2011) may affect tree vigour in different landscape positions. Although the ITR is similar to coastal forests with regard to climate, it is in the lower end of the coastal climate range for precipitation as rain (Stevenson et al. 2011). Outbreak severity is likely affected by host susceptibility that may be increased at higher elevations in the study area. Decreased precipitation increases moisture stress, which most likely contributes to host susceptibility (Figure 4-6 to 4-10). Although tree growth at upper elevation sites was not sensitive to increased summer temperatures (see Chapter 3), this decreased overall moisture combined with colder temperatures at upper elevations (and therefore less built up resources in trees to buffer defoliation), offers a possible explanation for the increased severity of upper elevation WHL outbreaks in this study.

No trends in outbreak frequency between upper and lower elevation sites were identified statistically. Given that the climate drivers for WHL outbreaks are warm and dry summers (McCloskey et al. 2009), upper elevation sites would be expected to experience fewer outbreaks due to lower temperatures. However, the actual differences in elevation between upper and lower sites were relatively small (Table 3-1) and temperature differences between elevations may not have been enough to cause significant differences in WHL outbreak frequencies. Frequency may be more tied to temperature requirements and temperature was not significantly different based on elevation in the study area. These temperature requirements may still exist, however the lack of a pattern determined through this study may reflect the broad elevational range of western redcedar occurring within the climatic range of WHL in the ITR. This could be because other variables such as high overall humidity (Arsenault & Goward 2000) attenuates extreme temperatures (and therefore the moisture stress index)

more than aspect or elevation and there wasn't enough elevational difference between upper and lower sites to have a significant effect on WHL outbreak development. In addition, this study found western redcedar growing at higher elevations to be less sensitive to increased summer temperatures (see Chapter 3), possibly explaining the lack of frequency trend based on elevation.

Outbreak frequency and severity was not significantly different between north- and south-facing sites, which is different than expected due to temperature requirements of WHL at various development stages (McCloskey et al. 2009). However there was no significant difference in temperature by aspect in the study area, which may explain the lack difference in outbreak dynamics between aspects. There was no significant difference in precipitation between aspects suggesting that moisture stress levels, and possibly host stress, were no different on north-facing versus south-facing slopes. This is supported by results in Chapter 3, which found that aspect had no influence on western redcedar's response to climate. While Kinghorn (1954) found that north-facing stands were more severely defoliated than south-facing slopes on Vancouver Island, other studies in the lower mainland of BC found that aspect had no significant effect on outbreaks (McCloskey 2007).

The most severe outbreak recorded began in or around 1834, with over half of all extant trees recording the outbreak. No clear trend could be identified in outbreak severity at the century scale when visually analyzed, indicating that outbreak severity has not increased over time. The second most severe outbreaks occurred in or around 1897 and 1992-1994, which were similar in severity. Figure 4-5 suggests a temporal pattern of severe outbreaks interspersed with less intense outbreaks. In the lower mainland of BC, the WHL return interval is 24.9 years with a range of 15 to 39 years (McCloskey et al. 2009), excluding less in-

tense outbreaks. In comparison to my reconstructions, outbreaks in the south occur at a higher frequency. A shorter growing season in the north may produce fewer years favorable to WHL development, producing a longer return interval. Outbreak frequency was relatively uniform across the 1800s and 1900s with three outbreaks in each century, indicating no change in frequency.

In sum, roughly 3 outbreaks per century, occurring approximately every 35.6 ±9.5 years occur in the ICHvk2 biogeoclimatic variant within the ITR, which is lengthy compared to other studies (McCloskey 2007). Outbreaks as shown appear to be cyclical in nature (Figure 4-5) and are preceded by particular climate variables as shown in this study (Figures 4-6 to 4-10). This is supported by general hypotheses about the cyclical nature of forest Lepidoptera (Myers 1988) which state that insect outbreaks in this order occur at regular intervals in susceptible areas across time, primarily caused by favorable climatic conditions. Outbreaks can be cyclical in severity or frequency as they occur due to cyclical climatic conditions or simply after the population has recovered after the last decline (Myers 1988). Although frequency of outbreaks has not changed significantly over the timespan of the study, this could change given warmer drier summers (Spittlehouse 2008) and predictions that WHL outbreaks may increase due to climate change in other parts of BC (McCloskey et al. 2009). Elevation is indicated to have a significant effect on outbreak severity, and neither elevation nor aspect has a significant effect on outbreak frequency, which does not appear to have changed over time. Elevation may be a threshold for WHL larval success as well as temperature limitation (as shown in Chapter 3).

4.4.2 Superposed Epoch Analysis

Results of superposed epoch analysis (SEA) were generally the same when analyzed grouped as July and summer moisture stress (June, July, and August). Elevated moisture stress (high temperatures combined with low precipitation) occurred in the third and second years prior to outbreaks, which could lead to increased larval success of WHL and aid populations to increase from the endemic to the epidemic phase, as insect growth is positively influenced by increased temperature (Larsson 1989). SEA based on temperature showed elevated temperatures preceding WHL outbreaks in the -3, -2 and year of outbreak, indicating an importance of temperature even in the year of outbreak, which is different than the results on moisture stress. The importance of elevated temperatures in the year of outbreak may correspond with the importance of elevated temperatures for increased WHL larval success, as seen in other species of Lepidoptera (Myers 1988), and the overall moisture stress in making western redcedar susceptible to WHL outbreaks (McCloskey et al. 2009). These findings are similar to those of climate-WHL studies in the lower mainland of BC (McCloskey 2007; McCloskey et al. 2009) where the third and second year prior to an apparent outbreak had the same elevated moisture stress index. It is possible that these climatic conditions occurred at other times within the timespan of the SEA; however WHL populations may be suppressed for a number of years following an outbreak due to the epizootic virus that contributes to population decline (Kinghorn 1954; McCloskey 2007). It is possible that WHL population sizes are primarily influenced by climate, but are limited during some years of favorable climatic conditions by other biological agents such as larval parasites and the epizootic virus, explaining why favorable weather conditions do not always yield WHL outbreaks at various times.

Elevated moisture stress levels were not observed in the year before outbreak occurrence, which is consistent with other studies in BC (McCloskey 2007; McCloskey et al. 2009). There are four possible explanations for this: 1) temperature is more important for WHL development than moisture stress; 2) due to the remote nature of the study area, it is possible that outbreak start years were incorrectly determined by forest managers and WHL populations started to increase dramatically before defoliation was evident; 3) the previous year's climate is influential in WHL larval success and is more important than the current year's conditions to WHL larval development; 4) that moisture stress is more important to host vigour and its ability to make defense compounds, resulting in the importance of the -3 and –2 years due to trees ability to store energy and buffer defoliation. Harris et al. (1980) found that larval counts in their coastal BC study area increased dramatically after the first year of visible defoliation, supporting the second explanation. Historic WHL outbreaks have been observed to build populations for multiple years before defoliation (Kinghorn 1954) (and therefore ring-width suppression), supporting the third hypothesis. The fourth explanation is supported by other research (Larsson 1989; Koricheva et al. 1998) that shows diminished tree vigour is positively correlated with host susceptibility and susceptibility to damage by herbivorous insects. In sum, high temperatures combined with limited precipitation lasting multiple years pre-occurred WHL outbreaks in the ICHvk2 biogeoclimatic subzone of the ITR, within the existing climatic dataset. This information, combined with outbreak frequency, allows for approximate prediction of future outbreaks.

4.4.3 Conclusions and Future Climate Change Implications

Given that WHL has been present in the study area since at least the 1700s, and probably earlier, future outbreaks can be expected. If the mean return interval holds true, another outbreak can be expected in the next 5-20 years. Climate change models predict future summer conditions to display lower than normal precipitation, with greater than normal temperatures (Spittlehouse 2006; Wang et al. 2006;), which would increase the magnitude and frequency of moisture stress un-favorable to western redcedar vigour and of high temperatures favourable to WHL larval development. Based on the results of this study, these changing future climatic conditions could potentially increase the frequency and severity of WHL outbreaks in the study area through an increase in frequency of years with conditions unfavourable to western redcedar vigour and favorable to larval development.

WHL outbreaks in the ICHvk2 biogeoclimatic variant of the ITR have occurred historically and most likely will continue to occur. Frequency could potentially increase, although there is no trend detected in this study. However; severity of events is likely to increase due to climate change based on this study and others who found that hot, dry conditions precede WHL outbreaks in BC (McCloskey et al. 2009). WHL is an important driver of stand dynamics, and forest managers will be able to use the information included in this study to develop management plans for the ITR that would help mitigate effects of climate change on disturbance caused by WHL.

Table 4-1. Number of trees recording reconstructed outbreaks, by site. The total number and percent of trees recording outbreaks across all sites is at the bottom of the table.

Site	1992 (n=266)	1954 (n=269)	1920 (n=238)	1897 (n=182)	1874 (n=123)	1834 (n=80)	1785 (n=31)	1741 (n=15)
1	6	14	1	9	3	3	1	0
2	4	1	6	5	0	10	1	0
3	10	1	2	4	1	4	4	1
4	9	4	6	8	0	1	0	0
5	8	0	3	1	0	0	0	0
6	2	4	3	2	1	1	0	0
7	2	2	11	2	0	2	1	0
8	1	17	0	11	3	6	2	1
9	7	3	4	7	0	2	0	0
10	2	2	1	17	5	6	1	0
11	8	1	0	2	1	2	0	0
12	20	0	2	4	0	2	0	1
13	11	8	3	7	1	6	0	1
Total	90	57	42	79	15	45	10	4
Percent	33.8	21.2	17.6	43.4	12.2	56.3	32.3	26.7

Table 4-2. Outbreak occurrence in mean site chronologies.

Site	Elevation (m)	1992	1954	1920	1897	1874	1834	1785	1741
1	1019		✓						
2	756						✓		
3	1139	✓					✓	✓	✓
4	738	✓					✓		
5	1006								
6	682								
7	667							✓	
8	916		✓		✓	✓	✓		
9	683						✓		
10	1005				✓				
11	820	✓					✓		
12	1240	✓							
13	802	✓							

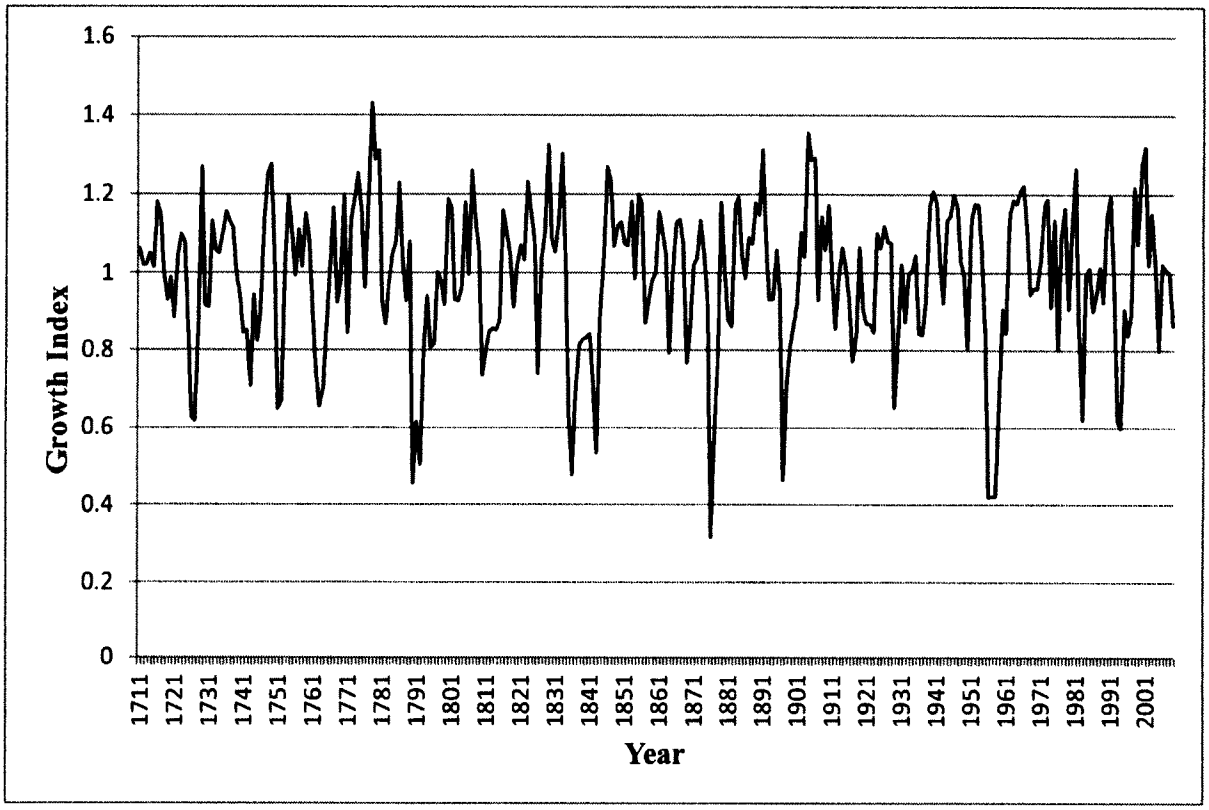

Figure 4-1. Standard chronology of site 1, for use in outbreak analysis.

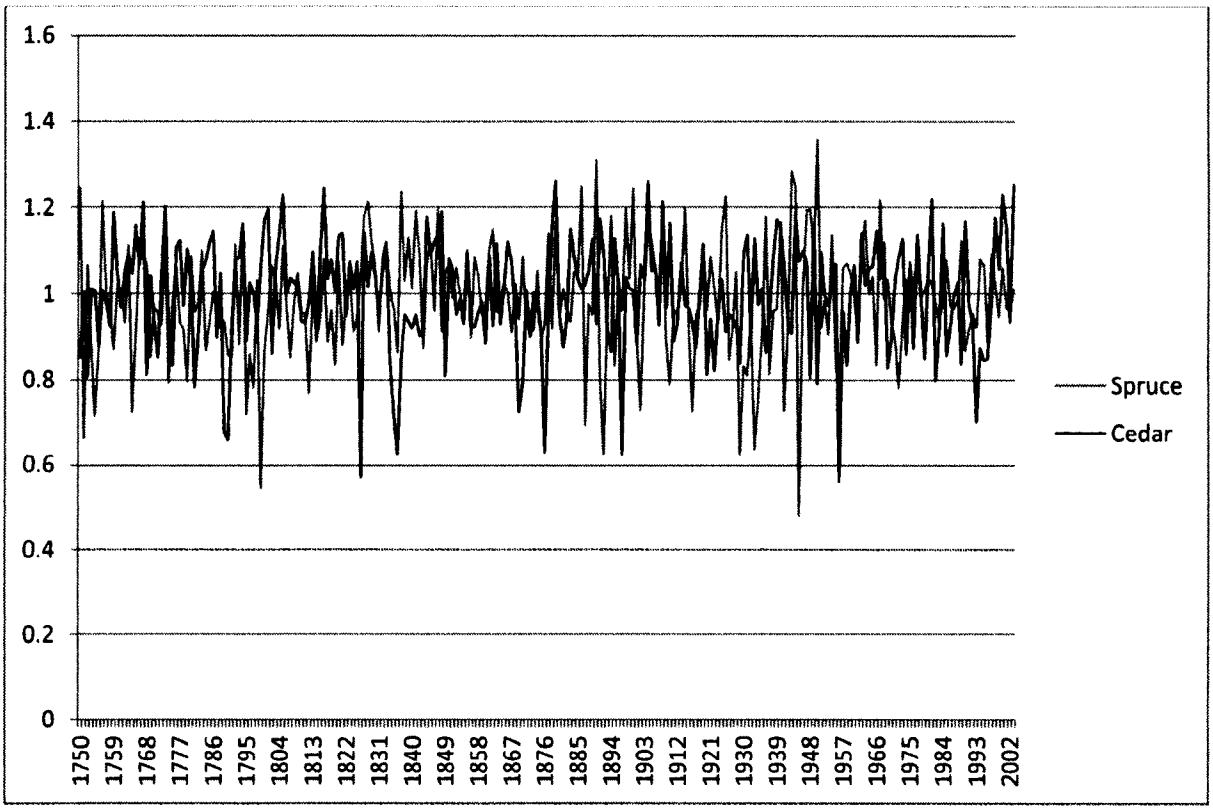

Figure 4-2. Residual chronologies from ARSTAN of Engelmann spruce control chronology and all western redcedar trees in the study area.

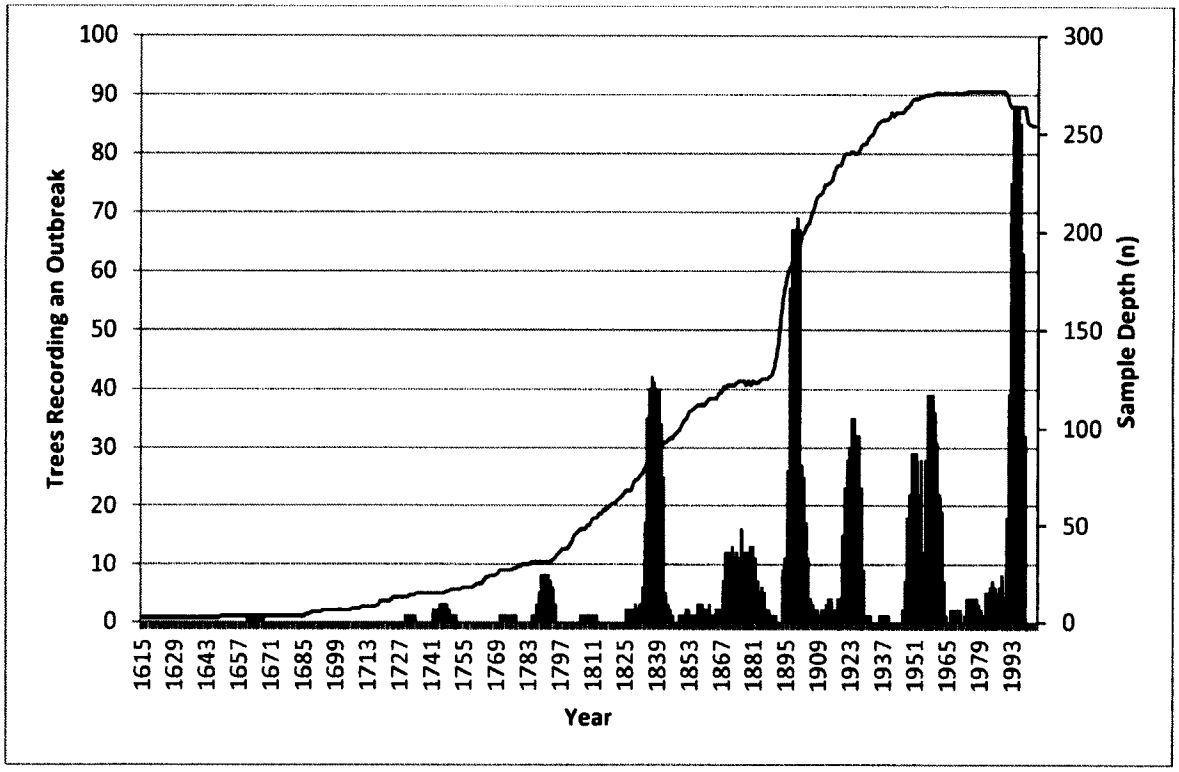

Figure 4-3. Total trees recording western hemlock looper outbreaks with sample depth (n) on secondary axis.

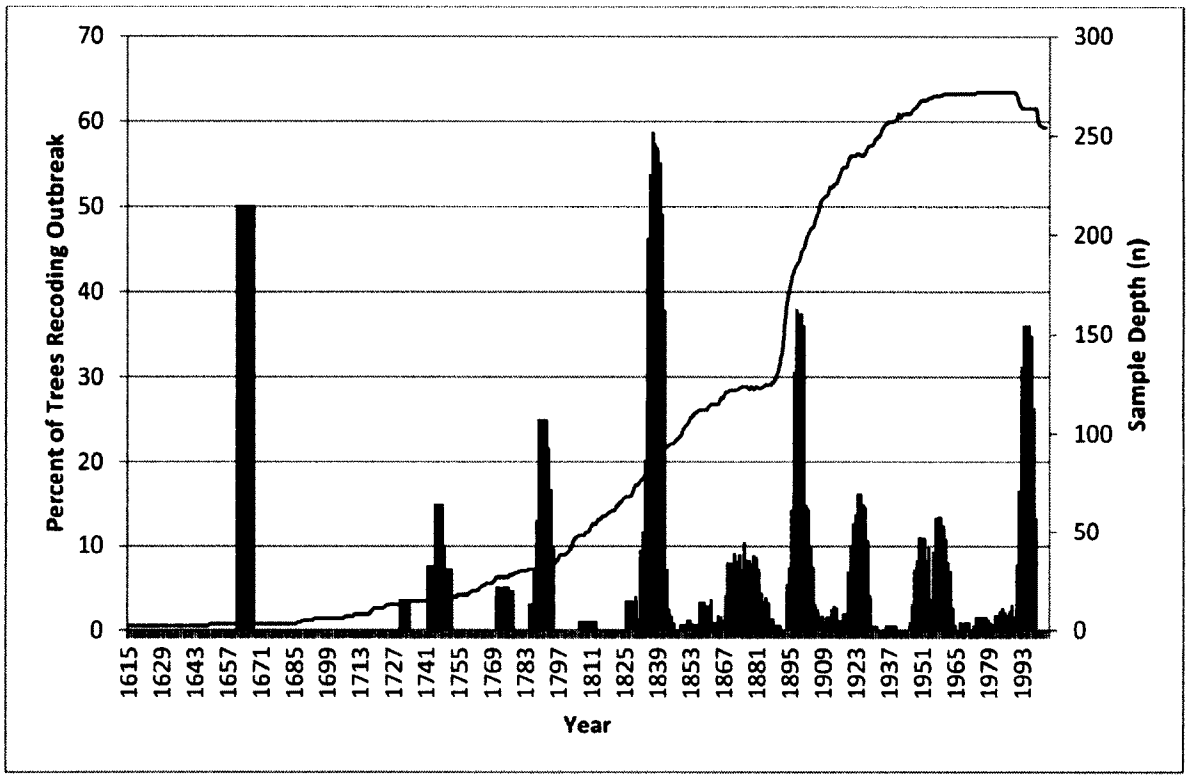

Figure 4-4. Total percent of trees recording outbreak with sample depth (n) on secondary axis.

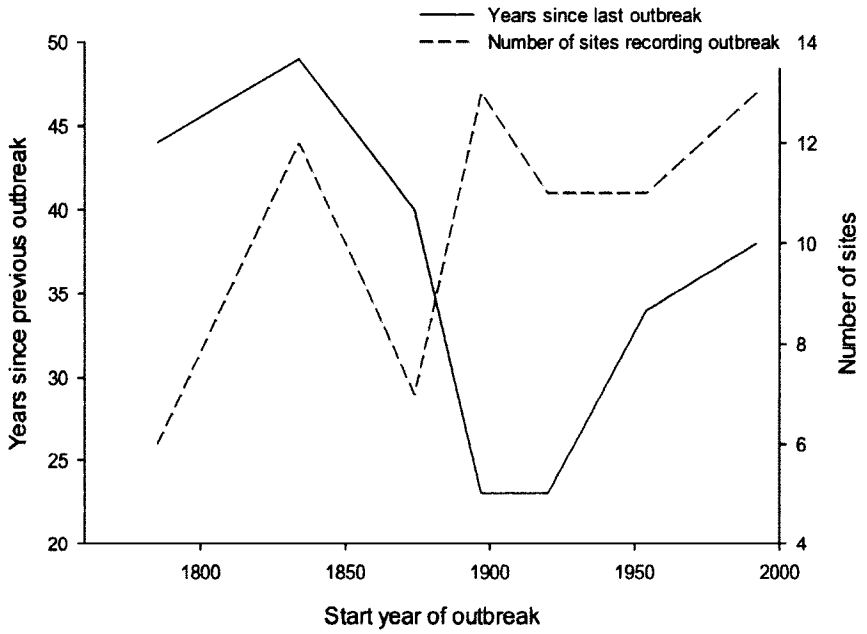

Figure 4-5. Years since last outbreak plotted at the start of the current outbreak (solid line). Number of sites recording an outbreak at the start of each outbreak period (dotted line).

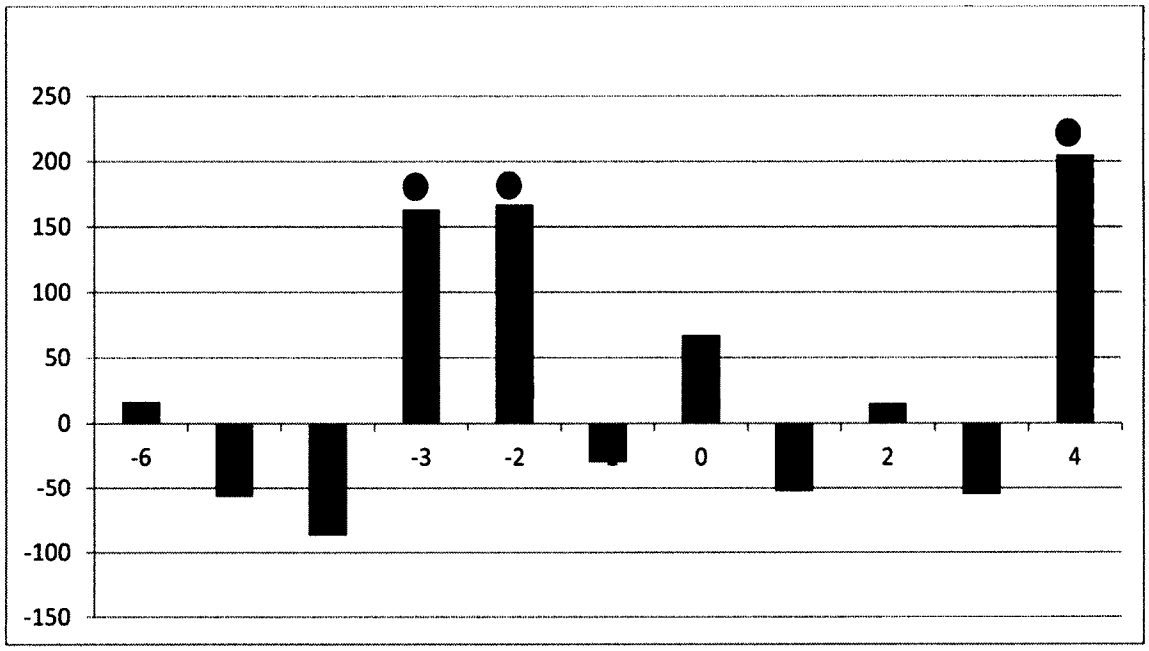

Figure 4-6. Superposed epoch analysis of July moisture stress index and outbreak years. Dots above the bars indicate significant correlations ($P < 0.05$).Axes represent z-scores.

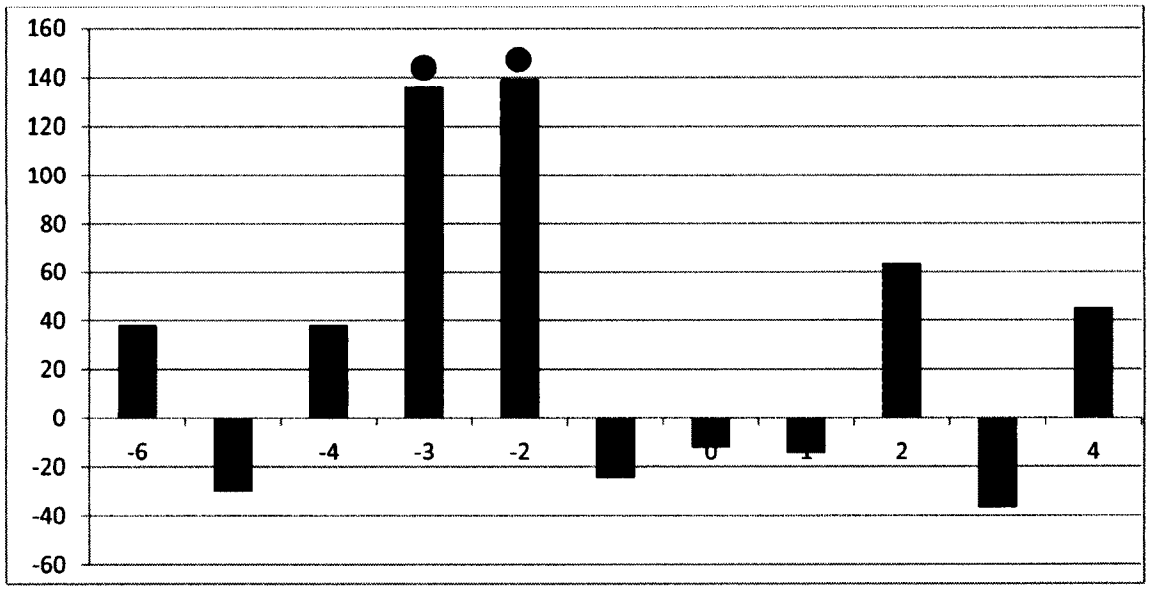

Figure 4-7. Superposed epoch analysis of seasonal (summer) moisture stress index and outbreak years. Dots above the bars indicate significant correlations ($P < 0.05$). Axes represent z-scores.

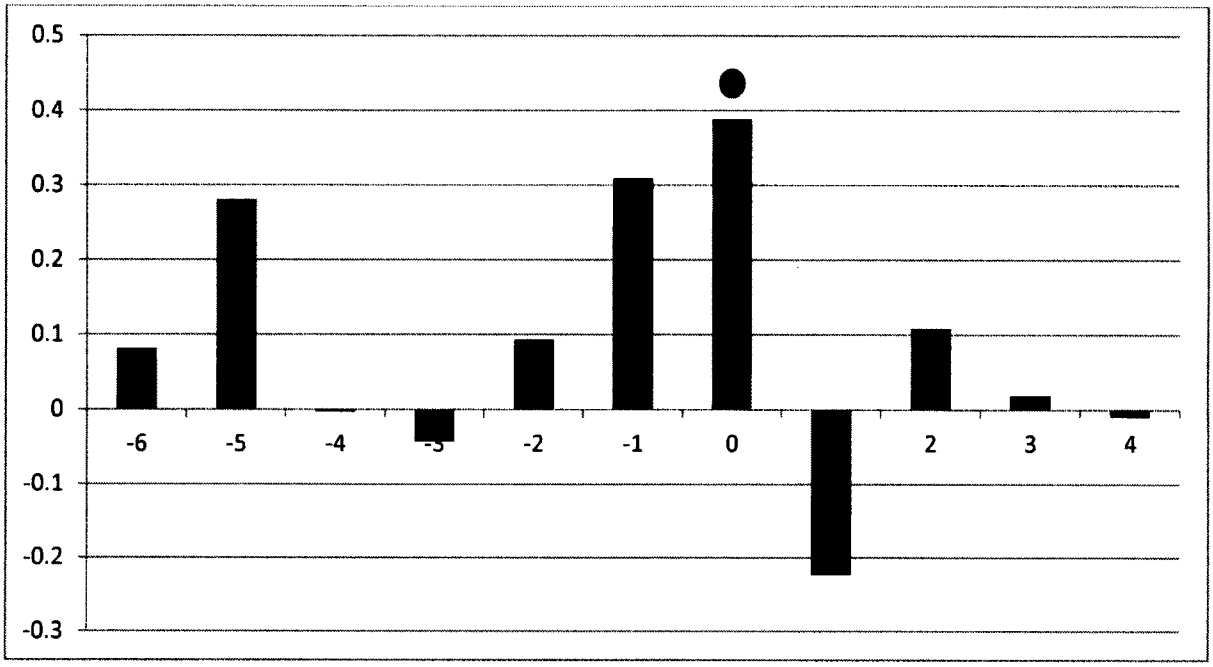

Figure 4-8. Superposed epoch analysis of annual temperature and outbreak years. Dots above the bars indicate significant correlations ($P < 0.05$). Axes represent z-scores.

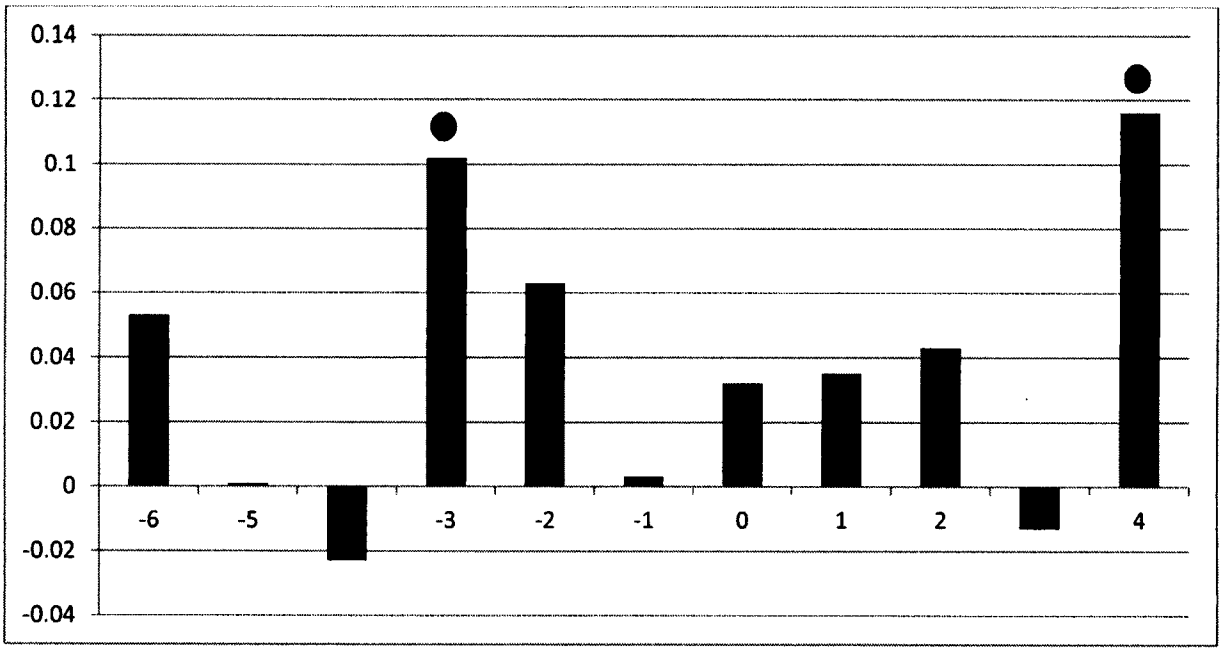

Figure 4-9. Superposed epoch analysis of July temperature and outbreak years. Dots above the bars indicate significant correlations ($P < 0.05$). Axes represent z-scores.

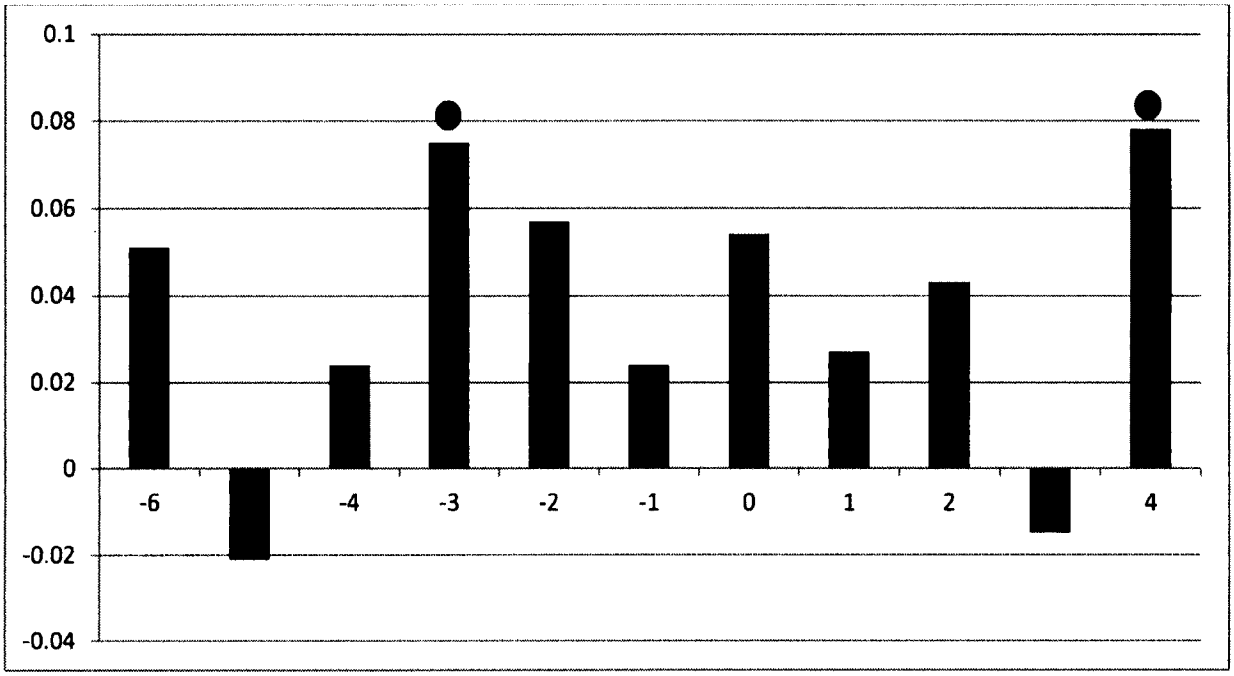

Figure 4-10. Superposed epoch analysis of seasonal (summer) temperature and outbreak years. Dots above the bars indicate significant correlations ($P < 0.05$). Axes represent z-scores.

CHAPTER 5. SENSITIVITY OF WESTERN REDCEDAR TO CLIMATE AND WESTERN HEMLOCK LOOPER IN BRITISH COLUMBIA'S INLAND TEMPERATE RAINFOREST: A SYNTHESIS

5.1 Introduction

The purpose of this chapter is to bring together the analysis of western redcedar's growth response to climate variables, historical WHL outbreaks, and climatic conditions that may contribute to WHL outbreaks, provide an integration of the interaction of all three elements and how future climate conditions may affect western redcedar survival and growth in the ITR, and why it all matters to forest managers and others.

5.2 Climate Interactions of Western Redcedar and Western Hemlock Looper

In sync with the same climatic variables that limit western redcedar, WHL outbreaks are preceded by similar conditions (i.e. elevated moisture stress that affects the host and temperature that affects WHL development) (Figure 4-6) as described in Chapter 4. Ample starch reserves in western redcedar have been speculated to buffer WHL outbreaks near the study area (Hoggett & Negrave 2002). Starch reserves are necessary to refoliate after WHL outbreaks because trees use built-up resources to survive events that deplete their resources or reduce their capability to function (Loehle 1988). Therefore, successive years of poor growth due to high moisture stress leads to a reduced ability of western redcedar to defend against WHL defoliation. The same climatic conditions that preceded WHL outbreaks in this study have been observed elsewhere in BC (McCloskey 2007) and provide evidence that WHL outbreak frequency may increase (McCloskey et al. 2009) with future climatic condi-

tions. Given that this study has shown western redcedar growth is negatively correlated with warm summers, WHL outbreaks may not only increase in frequency but western redcedar may not be able to survive defoliation as well as it has historically; effectively increasing outbreak severity.

Chapter 3 demonstrated that based on aspect alone, trees in the study area respond to climate variables relatively similarly, with no differences between north and south aspects. The WHL outbreak-reconstruction in Chapter 4 came to the same result. These results were likely due to the lack of significant difference in climatic variables at the different aspects as discussed in Chapter 4. Like WHL outbreaks, which varied in frequency at different elevational positions, western redcedar growth in the study area varied with elevation in response to maximum June temperature; lower elevation sites were more sensitive than upper elevation sites, showing that trees growing at lower elevations may be more sensitive to future climate change scenarios and therefore WHL outbreaks due to stress. In addition, as temperature increases, mid and high elevations may become more temperature-limited. Conversely, stands growing at higher elevations are likely to be affected by changes in climatic regime due to the increased incidence of severe WHL outbreaks as shown in Chapter 4, likely due to a short growing season and limited ability to build up starch reserves. It is possible that these effects of climate change on enhancing outbreak frequency or severity may be offset by warmer, wetter winters that allow trees to build up more reserves to rebound after WHL outbreaks due to a lengthening growing season. Stands growing at lower elevations, however, may be affected adversely by climatic change, and that is where increased damage and potentially mortality could occur with more frequent WHL outbreaks. Upper elevation western

redcedar stands are more likely to be affected by more severe future outbreaks, though frequency may not increase in those stands.

In chapter 3 it was established that western redcedar growth in the study area is negatively correlated with precipitation as snow in the early winter (Figure 3-8) and positively correlated with precipitation as rain throughout the growing season (Figure 3-9), indicating a requirement for ample growing season moisture supplied as in-season rain. Vigour is important for trees to build up starch reserves that serve to bolster the trees' defenses over time (Larsson 1989). The positive growth response of western redcedar to increased precipitation detected in this study is corroborated by studies in other parts of British Columbia that show western redcedar grows best on fresh to moist sites with ample rainfall (Kayahara et al. 1997; Klinka & Brisco 2009), and in fact are susceptible to drought stress. In Chapter 3 I showed that climatic variables are important at the monthly or seasonal scale so annual climatic modelling may not have the potential to accurately predict western redcedar response to climate.

In years of decreased rainfall, WHL outbreaks are more likely to be severe because western redcedar may be stressed and unable to produce starch reserves which it needs to survive (Koricheva et al. 1998) periodic WHL outbreaks. Another study in the lower mainland of BC found the same WHL outbreak climate drivers (McCloskey 2007) and predicted the same outcome of greater WHL outbreak frequency should future climatic conditions become drier (McCloskey et al. 2009). In essence, moist and mild growing conditions allow western redcedar to thrive and build resources. Under dry conditions, western redcedar is vulnerable to WHL defoliation due to reduced tree vigour, and in addition, the insect is at the same time more likely to thrive given warmer temperatures. Western redcedar has not suffered extreme amounts of mortality during WHL outbreaks (at least in sampled locations) in

the past under historic climate conditions. A possible explanation for this is mature western redcedar's resilience to western hemlock looper and hardiness to survive successive years of defoliation and poor climatic conditions occurring in tandem, as shown by the sites in this study where trees have survived multiple outbreaks in their histories (Figure 4-3 and 4-4). In addition, only mature western redcedar were sampled, which are known to suffer less mortality during WHL outbreaks than young stems (Thomson 1957), specifically near the study area where many sampled western redcedar were reported to have survived the 1992-1994 outbreak (Hoggett 1998; Hoggett 2000; Hoggett & Negrave 2002). It is possible that the trend of mature western redcedar surviving outbreaks will change in the future if western redcedar doesn't build enough starch reserves under future climatic conditions.

In chapter 4 it was shown that known and reconstructed western hemlock looper outbreaks were identified through three centuries (1900s, 1800s, and 1700s) with varying degrees of severity and number of trees recording an outbreak at a given sample site, as well as in total. The outbreak return interval was determined to be 35.6 ± 9.5 years. I demonstrated in chapters 3 and 4, that future climate scenarios of warmer, drier summers (Spittlehouse 2008) may increase the frequency of WHL outbreaks due to reduced vigour of western redcedar. This coupled with a decrease in western redcedar's ability to refoliate in response to defoliation may lead to an increase in severity and mortality among mature individuals during an outbreak.

5.3 Conclusions

Climate change may present new challenges to the sustainability of western redcedar in the ITR. Warmer, drier summers will cause elevated moisture stress (McCloskey et al.

2009), reducing host vigour and making western redcedar more susceptible to defoliation, increasing severity of WHL outbreaks. The increased temperatures could enhance larval success and cause more frequent WHL outbreaks. On the other hand, warmer, wetter winters (Wang et al. 2006) are positively related to western redcedar growth, and may reduce some of the negative effects of increased stress during the growing season. Future climate change implications for western redcedar and WHL in the study area are a matter of ecological trade-offs; if western redcedar's tolerance of warm and dry summers exceeds that of the tolerance for harsh winters, future climate change based on existing scenarios may be beneficial to growth, as well as western redcedar's ability to persist through WHL outbreaks. The intersection of increased WHL outbreaks with either weakened or strengthened western redcedar will determine whether future forest characteristics will significantly change.

There remains considerable uncertainty regarding the future of western redcedar in the ITR. The theoretic nature of climate models applied to future tree growth (Wang 2005) makes any predictions about future climatic conditions approximate. Secondly, the response of the epizootic virus that ultimately causes decline in WHL during outbreaks (Kinghorn 1954) is uncertain; it may play a role in outbreak prevention or suppression despite more hospitable climatic conditions. How western redcedar responds to climate in the ITR will vary based on the realization of future climatic conditions, which may be the same or different as currently modelled. WHL outbreak frequency and severity will also vary based on the actual future occurrence of seasonal temperature and precipitation variables. The fate of the northern ITR is of concern to managers and users of the forest for all of its values, both economic and social, as well as the rare flora, fauna, and species assemblages (Arsenault & Goward 2000). Based solely on modelled future climatic conditions, western redcedar will

experience more frequent and severe WHL outbreaks, but possibly could be more able to buffer the effects. Future research should entail detailed climatic studies at the elevational extremes of the ICHvk2 subzone to determine climatic differences and predict future conditions, and more intensive tree sampling to add to the body of knowledge about WHL outbreak characteristics.

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